THE MILLIPED FAMILY CONOTYLIDAE IN NORTH AMERICA, WITH A DESCRIPTION OF THE NEW FAMILY ADRITYLIDAE (DIPLOPODA: CHORDEUMIDA)

WILLIAM A. SHEAR

ABSTRACT

The milliped family Conotylidae in North America is revised; figures and descriptions of all known species are given. The new family Adritylidae is proposed for the genus *Adrityla* Causey.

Two new genera of conotylids are described: *Achemenides* (type species, *Conotyla pectinata* Causey) and *Plumatyla* (type species, *Conotyla humerosa* Loomis). Twelve new species of conotylids are described: *Conotyla extorris*, *C. personata*, *C. elpenor*, *C. smilax*, *C. ocypetes*, *C. aeto*, *C. vista*, *C. celeno*, *Taiyutyla napa*, *T. franeisca*, *Austrotyla borealis*, and *A. chihuahua*. Three new synonymies in the genus *Conotyla* are recognized.

The biology and zoogeography of the group is briefly discussed.

INTRODUCTION

The small millipeds of the family Conotylidae are poorly represented in most collections, though species are fairly common in the northern parts of the United States, and at higher elevations elsewhere. That the distribution of this interesting group is a relict of a previous, colder age seems beyond question. Several species occur in caves, and many are characteristic of high altitudes, reaching near the timberline in the Rocky Mountains of Colorado and Alberta and in the White Mountains of New Hampshire, while adjacent lowlands are poor in species and in individuals. In the middle Appalachians, a pattern of highly localized, rare, endemic species is now emerging. The importance of millipeds to zoogeographers was repeatedly emphasized by O. F. Cook, but attempts to use them have been few, probably due to the chaotic state of diplopod taxonomy. It is hoped that studies like this one will encourage zoogeographers and paleoecologists to utilize the excellent zoogeographic information presented in many groups of millipeds.

The family name Conotylidae was proposed by O. F. Cook in 1896 for the milliped genera *Conotyla*, *Trichopetalum*, *Scoterpes* and *Zygonopus*, first described in detail by Cook and Collins in 1895. Since its establishment, little revisionary work has been done on the taxonomy of this family despite the large number of additional names that have accumulated under it. Verhoeff (1932) realized that the Conotylidae, in the sense of previous work, was an unnatural assemblage, and removed some genera to his new family, Trichopetalidae; his paper was not noticed by American students. Chamberlin (1952) established the genus *Taiyutyla*, and several new species were added to *Conotyla* by Loomis (1939, 1943) and by Causey (1952).

Hoffman (1961), aware of Verhoeff's assignment of the genera *Trichopetalum*, *Scoterpes*, and *Zygonopus* to the Trichopetalidae, studied the gonopods of several species of *Conotyla* in detail. He reviewed previous studies of the conotylids, and

placed a number of the forms then in *Conotyla* into a new genus, *Sonoratyla*. *Taiyntyla* was also discussed, as well as Chamberlin's enigmatic genera *Zygotyla* (1951), *Cookella*, and *Bollmanella* (1941). Hoffman made no attempt under the circumstances (see section below on dubious names) to clarify the status of these latter three genera. At the same time, Causey (1961a) carried out a similar study, published earlier than Hoffman's, and proposed the genus *Austrotyla* for some of the species later included in Hoffman's *Sonoratyla*. Later in the same year, Causey (1961b) published the new genus, *Adrityla*, based on *Conotyla deseretae*. Although further papers on conotylid genera have been announced (Causey, 1961a), they have not as yet been published.

I wish to thank Dr. Richard Hoffman, Radford, Virginia, for suggesting this study and providing numerous specimens and much unpublished data. His advice has been greatly appreciated. Dr. Nell Causey, Baton Rouge, Louisiana, loaned her collection of Conotylidae, probably the largest and most representative in existence, and made many helpful suggestions. H. F. Loomis, Miami, Florida, loaned unpublished drawings of new related taxa. Dr. Herbert W. Levi, Museum of Comparative Zoology, Cambridge, Massachusetts, read and edited the manuscript and loaned material from the collections under his care. Dr. Ralph Crabill, U. S. National Museum, loaned important type specimens. Dr. Andrew A. Weaver, Wooster, Ohio; Mr. Robin Leech, Edmonton, Alberta, Canada; Mr. Michael Gardner, Davis, California; and, Mr. Erik Thorn of the British Columbia Provincial Museum, Victoria, British Columbia, Canada, also loaned or donated important specimens. Mr. Stewart Peck of the Museum of Comparative Zoology loaned specimens and unpublished data, and contributed much to my understanding of the biology and evolution of the cave forms in the Conotylidae. All types of new species described herein are deposited in the Museum of Comparative Zoology.

TAXONOMIC POSITION OF THE FAMILY CONOTYLIDAE

The affinities of the Conotylidae lie primarily with three North American families (one briefly described as new, below) and with a poorly known group of Asian and South American species. Verhoeff (1913) placed *Japanosoma* (Japan) in the monotypic subfamily Japanosominae, and *Eudigona* (Chile) in the subfamily Eudigoninae of the Conotylidae. Neither of these subfamilies has been restudied since their original proposal, and their position remains in doubt. However, judging from the published data, they seem to be typical conotylids. The Asian family Diplomaragnidae is somewhat more distantly related to the Conotylidae (Verhoeff, 1942; Hoffman, 1963). Recently, Buckett and Gardner (1967) have described a new monotypic family, Idagonidae, type genus *Idagona*, from caves in Idaho. They stated that the new family was related to both the Conotylidae and the Cleidogonidae, but as I have earlier pointed out (Shear, 1969), the Conotylidae and the Cleidogonidae are not at all closely related to each other. The single major distinction between the Conotylidae and the Idagonidae lies in the loss of the telopodite articles of the posterior gonopods (ninth legs) in the Idagonidae; except for this, *Idagona* might be considered as an aberrant conotylid genus.

The relationship of the Conotylidae to the Trichopetalidae is somewhat problematic. The two families are quite similar in general body plan, but there is a distinct morphological gap in gonopod structure. The anterior gonopods of the conotylids are fused into a single article; those of the trichopetalids are two-articled, with a prominent coxite. A colpocoxite is lacking in the posterior gonopods of trichopetalids, which are two- or three-articled in all known forms; conotylids have a large

colpocoxite on the three-articled posterior gonopods.

Milliped gonopods are developed from walking legs, and there is a well-recognized tendency for more primitive forms to have the gonopods more closely resembling legs; reduction and fusion of segments is considered a specialized character. Thus, the Trichopetalidae seem a more primitive stock than the Conotylidae. Moreover, the conotylids have relatives in Asia and in South America, indicating possible dispersal routes into North America from either of these regions (or the reverse), while the trichopetalids, like the cleidogonids, are peculiarly North American. My own feeling is that judgment should be reserved pending a study of the Trichopetalidae; it is quite likely that the resemblance between them and the conotylids is due in great part to parallelism, or that trichopetalids are nearer an ancestral stock than conotylids. The problem is aggravated by the obviously derived trichopetalid characters of reduction in segment number, loss of at least some ocelli, and minute size, all of which contrast with the seemingly more primitive gonopod plan.

The following key will serve to separate the North American milliped families that may be confused with the Conotylidae. All of the families have in common swollen lateral segmental shoulders and greatly enlarged segmental setae; the male gonopods superficially resemble each other.

Key to Conotylidae and Related Families in North America

1a. Telopodites of ninth legs of males absent, ninth leg represented by the simple, subtriangular colpocoxite, which curves around the larger telopodites of the anterior gonopods; caves in Idaho ..... Family IDAGONIDAE

1b. Telopodites of ninth legs of males present but reduced, distal articles enlarged and turned dorsally 2

2a. Tenth legs of males with the coxae greatly enlarged and lobed, tenth telopodite reduced to two or three segments; anterior gonopods a pair of cheirites formed by fusion of telopodites, sternites, and tracheal apodemes ..... Family ADRITYLIDAE, new

2b. Tenth legs with the coxae only slightly enlarged, not lobed; anterior gonopods with telopodites free from the sternites 3

3a. Ninth male legs with a conspicuous colpocoxite, telopodites two-articled, the distal article oval and enlarged; anterior gonopods a single article; segmental setae usually less than one half the body width ..... Family CONOTYLIDAE

3b. Ninth male legs without colpocoxites, telopodites usually a single article often with conspicuous constrictions, often with a claw; telopodite of anterior gonopods two-articled; segmental setae frequently more than one half the body width ..... Family TRICHOPETALIDAE

A detailed study of the gonopod structure of *Adrityla deseretae* (Chamberlin) has convinced me that it should not be retained in the Conotylidae, as to retain it would make the family obviously polyphyletic. The new family Adritylidae, briefly characterized below, is probably related to the Conotylidae to about the same degree as is the Trichopetalidae. By even the most conservative criteria, the structure of the gonopods of *Adrityla* excludes it from any known chordeumoid family, though there is a vague resemblance to *Marquetia* (Opisthocheiridae; Brölemann, 1935: 278); I have not seen specimens of *Marquetia*.

Family ADRITYLIDAE new family

Type genus. Adrityla Causey, 1961; type species *Conotyla deseretae* Chamberlin, by original designation and monotypy.

Diagnosis. Large chordeumid millipeds (to 25 mm long) with 30 postcephalic segments, segmental setae and paranota prominent, head not covered by collum. Male gonopods modified from three interlocking pairs of legs; anterior gonopods (eighth legs) consisting of pair of cheirites formed from fusion of telopodite, sternite and tracheal apodeme of each side; posterior gonopods (ninth legs) three-segmented, coxae with large colpocoxite, partially fused to sternites and tracheal

apodemes, distal telopodite article inflated, turned dorsally. Tenth legs with coxae greatly enlarged and lobed, coxal gland present, coxae fused to sternites, telopodites reduced. Eleventh legs without coxal glands.

Notes. The single known species, *A. deseretae*, is common in canyons of the Wasatch Mts., Utah. The reader is referred to the paper of Causey (1961b) for further details.

Family CONOTYLIDAE Cook

Conotylidae Cook, 1896, Brandtia, No. 2, p. 8. Verhoeff, 1932, Zool. Jahrb. Abt. Syst., Vol. 62, p. 500. Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 263.

Type genus. Conotyla Cook and Collins, 1895.

Diagnosis. Small to medium-sized (9–25 mm) chordeumid millipeds with 30 postcephalic segments. Head not covered by collum. Eyes present, in triangular patch, sometimes reduced in size and number from maximum of 22–24. Antennae with third article longest, proportions of other articles variable; not markedly clavate; long and slender. Sensory cones four or five. Mouthparts typical. Mentum not divided, mandibles with about 12 pectinate lamellae. Post-collum segments with prominent lateral swellings bearing outer two segmental setae on each side. Segmental setae large, prominent, movable. Epiproct and periprocts truncate; spinnerets two. Legs long, slender, claws prominent, basal segments heavily setose-pilose. Legs one and two of males reduced in size, six-segmented; legs three through seven longer than postgonopodal legs, usually thickened and crassate, often with strong knobs on some of the segments. Gonopods modified from eighth and ninth legs; anterior gonopods consisting of single article, sternum variable. Posterior gonopods three-jointed, coxa free from sternum, with large colpocoxite, distal telopodite article inflated, turned dorsad, without a claw. Coxae of tenth legs with large coxal glands, coxae sometimes lobed. Coxae of eleventh legs without glands, sometimes with prominent hooks. Prefemur of eleventh legs with prominent hooks. Remaining legs unmodified. Female cyphopods of two valves opening anteriorly at rest, pore of oviduct covered by single receptacle.

Distribution. North America, Japan, Chile.

BIOLOGY OF THE CONOTYLIDAE

Little is known of the biology and ecology of the Conotylidae. In southeastern West Virginia, immature specimens were frequently taken from leaf litter and rotted wood by Tullgren funnel sampling during the summer and early fall. However, nearly 90 percent of all examined collections of mature specimens, including those from caves and high altitudes, were taken between the months of November and April. Cook and Collins (1895) commented on the surprising activity of *Conotyla* during the winter, and I have seen mature specimens of *Conotyla* walking briskly over frozen logs and ice crystals. In addition, most of the records known to me from the eastern part of the continent are either from caves, high altitudes, or cool microclimates supporting such trees as hemlock, spruce, and fir. In the Rocky Mountains of Colorado, all but a few records of *Austrotyla coloradensis* are from coniferous forest above 7000 ft. (2500 m) elevation. *Conotyla albertana* has been collected in Alberta in alpine meadows above 6500 ft. (2150 m), and no records below 4200 ft. are known. *Austrotyla specus*, *Conotyla blakei*, and *C. bollmani* are found at low elevations in the interior of the continent, but most reliable records are from caves. *Achemenides pectinatus* and *Plumatyla humerosa* are known only from caves, and the latter is the only conotylid showing well-marked cave adaptations.

Howden (1963) has pointed out that animal species populations may adjust to a warming climate by persisting in cooler microhabitats (caves, mountain-tops), or

by adjusting their major period of activity to the cooler part of the year. The evidence above seems to indicate that, following Quaternary glaciations, both adjustments may have been made by various species of conotylids.

The distributions of *Conotyla blakei* (Map 2) and of *Austrotyla specus* (Map 3) may reflect a current period of cave invasion and northward movement following the Wisconsin glaciation and subsequent retreat. Barr (1968), in an excellent summary of the evolution of troglobitic animals, points out that the isolation and evolution of a troglobite usually is preceded by a stage during which an ancestral species is troglophilic. The small cave populations are occasionally swamped genetically by invasions from the surface population. Isolation and subsequent speciation occurs when the surface populations are eliminated by some (usually climatic) change that does not significantly affect the environmental conditions in the caves. Because populations in caves are small, genetic drift and founder phenomena play a great part in their evolution (Barr, 1968: 82–84). Although present *Conotyla* and *Austrotyla* cave populations seem to be geographically isolated from large surface populations, no appreciable differentiation has taken place. Perhaps more thorough surface collection in the regions of cave records will produce evidence of populations that can produce the swamping effect.

However, it must not be overlooked that it is the maxima and minima of climatic parameters, not the average, that usually restrict the range of a species. In the case of *Achemenides pectinatus*, caves may have served as refugia from the severe periglacial climate during the glacial maxima. A further difficulty is posed by the wide distribution in California of *Plumatyla humerosa*, a true troglobite. More than one species may be represented in the numerous collections of immature specimens.

I have made extensive personal observations on the ecology of only a single species, *Conotyla blakei*. About 20 specimens of both sexes were observed and collected on Mt. Equinox, Bennington Co., Vermont, and Mt. Greylock, Berkshire Co., Massachusetts. All specimens were taken from above 3000 ft. (1000 m) in elevation, in dense fir forests. The Mt. Equinox populations were observed in October, 1968, and May, 1969; those on Mt. Greylock in May, 1969. Without exception, the animals were found under the bark of dead standing trees or fallen logs. The bark was loosened to the extent that it could easily be peeled off in large slabs, and the wood underneath, on which the animals were usually resting, was saturated and soft—water could easily be squeezed from it by the fingers. Held in the hand or exposed to sunlight, the millipeds reacted by curling the head and first few segments under the body and withdrawing the legs into a position parallel with the long axis. After a few seconds, a period of rapid running and searching followed. If not allowed to find shelter from the sun, or if not released from the hand, the millipeds became immobile and moribund in a matter of 30 seconds. Similarly, an attempt to keep *C. blakei* in the laboratory resulted in the death within 24 hours of all individuals collected, even though high humidity was maintained. Presumably, temperature was a major factor in the laboratory and field deaths.

A single mating was observed in May, 1969, on Mt. Equinox, at an elevation of about 3800 ft.; there were numerous persistent snowbanks in the fir thicket where the mating pair was found. The female held onto the wood of the rotted tree-trunk with the last 10 or 12 segments, while the male coiled about her body, using the crassate first seven pairs of legs to embrace her head and anterior segments. No thrusting movements of any sort were observed, but the pair experienced difficulty in separating after being disturbed.

Schubart (1934) reported spermatophore

formation and transfer in some European chordeumids. In these forms, the male secretes sperm from the seminal pores on the coxae of the second legs into coxal sacs on the postgonopodal legs (in the case of the conotylids, these sacs are found on the tenth legs only). The secretions from these glandular sacs then form the seminal fluid into a spermatophore (Fig. 34) which, during mating, is transferred to the female cyphopods (Fig. 15) at the bases of the second legs by the gonopod complex (Fig. 14) of the male. In preserved male specimens of conotylids, these coxal sacs on the tenth legs are often extruded. In several cases, two large globular objects were attached to the extruded ends of the coxal sacs. These were easily detached, and examination under a compound microscope showed that each consisted of a cemented mass of small cells. This structure may represent a spermatophore. If this is the type of mating behavior that occurs in the family, then the distinction in gonopod function pointed out for other families by Brölemann (1935) and referred to by Hoffman (1961) may be applicable to conotylids.[1]

Feeding presumably takes place as in other chilognath millipeds, material being scraped or picked up from the substrate by a combination of movements of the gnathochilarium and mandibles, and ground by the dentate and pectinate lamellae of the mandibles. The finely triturated material in the foreguts of several *C. blakei* was composed of wood tracheids and fungal hyphae.

Molting and oviposition have not been observed, but some North American chordeumids make silk chambers for these purposes.

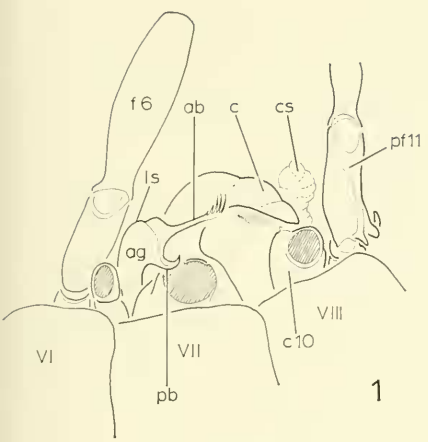
[1] Because of some uncertainty, I have not used the terms *paragonopod* and *peltogonopod* (see Hoffman, 1961) but have used the more understandable, though less specific, terms *anterior gonopods* to indicate those modified from the eighth legs, and *posterior gonopods* to indicate those modified from the ninth legs.

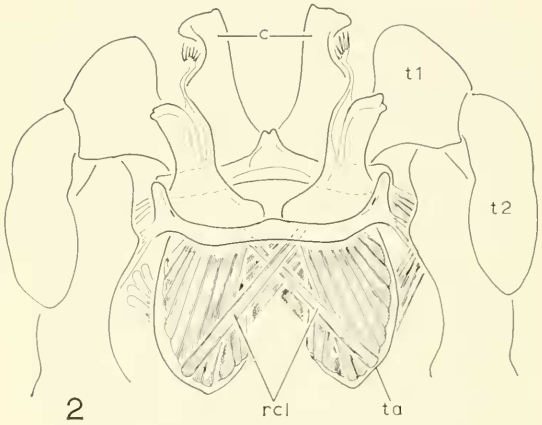
TAXONOMIC CHARACTERS AND GONOPOD STRUCTURE

Unfortunately, as is true of many milliped groups, nonsexual characters are of very little use in separating species, and even genera. Causey (1961a) attempted to use the relative lengths of the antennal segments in some species of *Austrotyla*, but such meristic characters must be used with caution when few specimens are available. In species that occur both in and out of caves, ocelli number and arrangement is variable, or it is the same in related epigean species, so that this character is usually of little value. Nonetheless, since such characters may at some time be useful, I have described them for all the species mentioned here. I have, however, omitted much of the usual detail from the species descriptions, particularly description of structures which are common to all members of a family or genus.

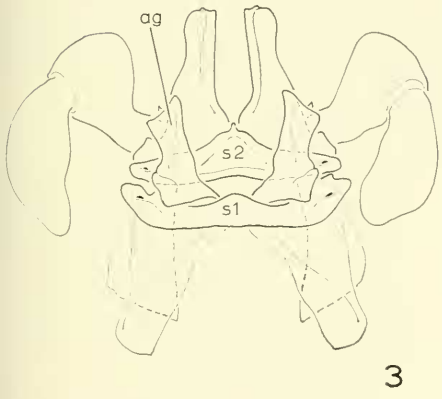
Also, female specimens are difficult to assign to species, and even genus. The cyphopods, useful in other chordeumid groups, are virtually identical in different species of Conotylidae. In addition, they are generally so poorly sclerotized that they shrivel when preserved, further reducing their utility in taxonomy. The best taxonomic characters are to be found in the male gonopods. In addition, the modifications of some of the pregonopodal legs of the males, usually taking the form of mesal lobes on one or two segments, are quite important in separating species.

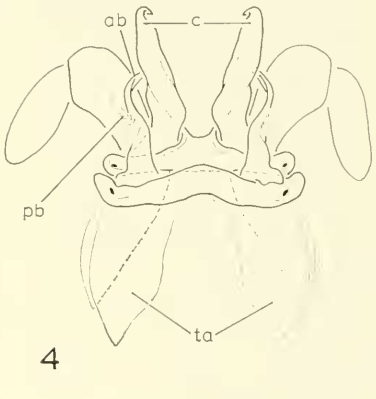
Conotyla melinda (Figs. 1, 2) has gonopods typical in many respects of the large group of Appalachian species which are highly endemic in their distribution. In lateral view (Fig. 1) the anterior gonopods are seen to curve laterad of the colpocoxites *(c)* of the posterior gonopods (telopodite articles of posterior gonopod not shown). The apex of the anterior gonopod is divided into two branches, an anterior branch *(ab)* and a posterior branch *(pb)*, and there is a prominent lateral shoulder *(ls)* on

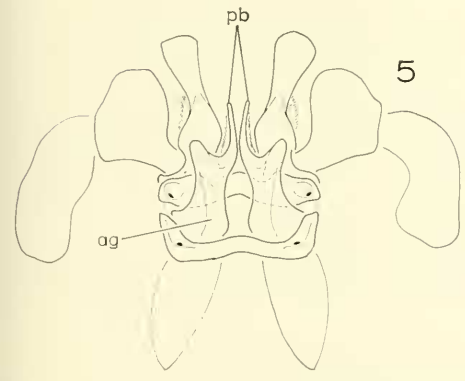


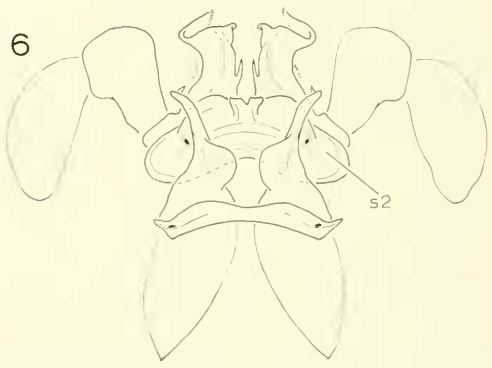


0.5 mm









Figures 1–6. Anatomy of conotylid male gonopods. Fig. 1. *Conotyla melinda*, lateral view. Fig. 2. *C. melinda*, anterior view. Fig. 3. *C. fischeri*, anterior view. Fig. 4. *C. blakei*, anterior view. Fig. 5. *C. smilax*, anterior view. Fig. 6. *C. latrolineata*, anterior view.

which, in some species, the process of the femur of the seventh leg rests *(Conotyla vista,* Fig. 41). Note also the coxal sac of leg ten *(cs)* and the modified prefemur of leg eleven *(pf 11).* In an anterior semidiagrammatic view (Fig. 2), the narrow, bandlike sternum of the anterior gonopods is visible, as well as the telopodite articles of the posterior gonopods. Hoffman (1961) showed that the narrow muscle *(rcl)* known as the remotor coxae longus, extending from the distal part of the tracheal apodeme *(ta)* to the base of the anterior gonopod, can be used to establish the homology between that portion and the coxa of a walking leg. Thus, the anterior gonopod is a coxotelopodite articulating directly with its sternum. In *Conotyla fischeri* (Fig. 3), a similar pattern is repeated, but the anterior branch of the anterior gonopod *(ag)* is usually not developed. This branch is typically plumose when present. *Conotyla blakei* (Fig. 4) is representative of a group of species with somewhat simpler gonopod construction. The anterior branch *(ab)* of the anterior gonopod is reduced to a poorly sclerotized plumose rod that is broken off in many specimens, and the posterior branch *(pb)* is a smooth continuation of the gonopod mass. There is no lateral shoulder. The colpocoxites *(c)* are likewise simpler in form (Fig. 17). The sterna are somewhat broader in this species than in the central Appalachian group. *Conotyla similax* (Fig. 5) is a slightly aberrant Appalachian form in which the anterior gonopods *(ag)* do not pass laterad of the colpocoxites *(c),* and bear no posterior branch. The colpocoxites (Fig. 31) are complex on the posterior surface, with a terminal process *(tp),* mesal tooth *(mt),* lateral notch *(ln),* and pilose area *(pa).*

Conotyla atrolineata (Fig. 6) differs from the eastern North American species of *Conotyla* in the simplification and reduction of the anterior gonopods, the broadening of the sternum of the posterior gonopods *(s),* and the much greater complexity of the colpocoxites (Figs. 48, 49, 50). This trend culminates in the related species, *C. albertana,* with an exceptionally broad posterior gonopod sternum (Fig. 7).

In *Taiyutyla corvallis* (Fig. 8), the anterior gonopod sternum *(s)* is heavily sclerotized and not bandlike, completely encircling the simple, platelike anterior gonopods *(ag),* which are larger than the colpocoxites *(c).*

In *Austrotyla coloradensis* (Fig. 9), the sternum of the anterior gonopods *(s)* may, in certain preparations, appear divided, though it is in reality a single piece encircling the gonopods and nearly meeting posteriorly. Lateral extensions of this sternum articulate with the lateral surface of the gonopod, which is simple and leaflike and larger than the colpocoxite. The colpocoxite *(c)* is usually cupped anteriad and may have two parts. The tracheal apodemes are reduced in size.

Plumatyla humerosa (Fig. 10) is a unique form somewhat intermediate between *Taiyutyla* and *Austrotyla,* but the lateral extensions of the solidly constructed sternum *(s)* are more firmly fused to the gonopod than they are in either of the preceding. The anterior gonopod *(ag)* is complex (Fig. 80), with two branches perhaps homologous to the two branches found in many *Conotyla* species. The colpocoxites *(c)* are remotely similar to those of *Austrotyla.*

Achemenides pectinatus (Fig. 11) differs in most respects from the other members of the family. The anterior gonopod sternum *(s)* is truly divided, and each sternite is doubled over longitudinally (Figs. 54, 55). The anterior gonopods *(ag)* are fused at the base, and are much larger than the colpocoxites *(c),* which are widely separated on a thin, bandlike sternum. The tracheal apodemes of the posterior gonopods are small and bifurcate.

PROBLEMATICAL NAMES IN THE CONOTYLIDAE

Due to the fact that the male genitalia are the only reliable specific characters in

this family, names based on females and on immature specimens are extremely difficult to assign, particularly if more than one species of conotylid occurs in the region. In two cases, *Conotyla wyandotte* (Bollman) and *Conotyla jonesi* Chamberlin, I have made some attempt to place names attached to females or lost specimens in the proper synonymy.

Listed below are the problematical names, with brief discussions of their original proposals and histories.

Cookella leibergi (Cook and Collins)

Conotyla leibergi Cook and Collins, 1895, J. New York Acad. Sci., 9(1): 77, figs. 102–104.
Cookella leibergi, Chamberlin, 1941, Bull. Univ. Utah, Biol. Ser., 6(5): 13.

This species was originally described from a female (holotype in U. S. National Museum, examined), which was supposed to have a small, broadly triangular prementum. This mistaken original observation of Cook and Collins (1895) was used by Chamberlin (1941) as a pretext for erecting the completely unnecessary genus *Cookella*. The type locality, [the shore of] Lake Pend d'Oreille, Idaho, could be within the range of either *Conotyla atrolineata* or *C. albertana*, and *leibergi* would thus be treated either as a junior synonym of *atrolineata* or the correct name for *albertana*. Loomis (personal communication, 1968) has in preparation descriptions of new taxa from the Idaho-Montana area; *leibergi* males may conceivably be represented among them. As neither the generic or specific name can be properly dealt with in the absence of males, I consider *Cookella leibergi* a *nomen dubium*.

Trichopetalum glomeratum Harger

Trichopetalum glomeratum Harger, 1872, Amer. J. Sci. Arts, 4: 118.
Conotyla glomerata, Cook and Collins, 1895, J. New York Acad. Sci., 9(1): 78.

The holotype, from the John Day Valley, Oregon, has been lost, and as Cook and Collins (1895) stated, the original description is too vague to allow definite placement, though a certain similarity to *Taiyutyla* emerges. It is probably neither a *Trichopetalum* nor a *Conotyla*. I consider it a *nomen dubium*.

Bollmanella oregona Chamberlin

Bollmanella oregona Chamberlin, 1941, Bull. Univ. Utah, Biol. Ser., 6(5): 12.

The male holotype, from John Day Creek, Douglas Co., Oregon, is reputedly in the Chamberlin collection at the University of Utah, but it could not be located by the curator there. There is nothing diagnostic about the description of the genus or of the type and only species, which even contradict one another in the matter of a lobe on the fourth article of the fifth legs. No illustrations were presented. I consider it a *nomen dubium*.

Zygotyla phana Chamberlin

Zygotyla phana Chamberlin, 1951, Nat. Hist. Misc. No. 87: 7–8, fig. 14.

The holotype, from Blue River, British Columbia, Canada, is obviously immature, having only 28 segments and undeveloped gonopods ["The gonopods seem to have been broken off in the type (Chamberlin, 1951)."] Though the type was to have been placed in the Provincial Museum of British Columbia, they have never received it, and it could not be located in the Chamberlin collection at the University of Utah. Geographically, this species could possibly be a synonym of *C. atrolineata*, but it may also represent an undescribed species. *Nomen dubium*.

Conotyla jonesi Chamberlin

Conotyla jonesi Chamberlin, 1951, Nat. Hist. Misc. No. 87: 7, fig. 13.

The drawing given by Chamberlin (1951) for *C. jonesi* is very much like *Taiyutyla corvallis* when properly oriented; the type localities (type of *T. corvallis* from Corvallis, Oregon) are only about 25 miles apart and both are in the Willamette River

valley. None of the characters given in the original description of *C. jonesi* are in the least diagnostic; they could apply to almost any conotyloid of the region. See Hoffman (1961) for a full discussion of Chamberlin's errors of observation in the description of *T. corvallis*. The type of *jonesi* was supposedly placed in the Provincial Museum of British Columbia, but they have no record of ever having received it, and it could not be located in Chamberlin's collection at Salt Lake City. At any rate, if specimens from the type locality of *jonesi* prove to be identical to *corvallis*, the name may have to be changed to *jonesi*, which has a year's priority. For the present, *jonesi* is best regarded as a *nomen dubium*.

KEY TO GENERA OF CONOTYLIDAE OF NORTH AMERICA

1a. Anterior gonopod sternum divided; anterior gonopods fused to each other at base, much larger than colpocoxites of posterior gonopods (Fig. 10); northern Illinois, northeastern Iowa, southwestern Wisconsin ..... *Achemenides*

1b. Anterior gonopod sternum not divided (Figs. 1–9); anterior gonopods not fused to each other, though they may be closely appressed, smaller or larger than colpocoxites of posterior gonopods 2

2a. Anterior gonopods flattened, platelike, often appressed in the midline (Figs. 8, 9), larger than or subequal to colpocoxites of posterior gonopods 3

2b. Anterior gonopods never flattened, often with complex or plumose branches (Figs. 1, 32–34), smaller than or subequal to colpocoxites of posterior gonopods 4

3a. Anterior gonopod sternum with lateral processes partially fused to lateral sides of coxotelopodites (Fig. 69); coxotelopodites complex on posterior surface (Fig. 78); colpocoxites small, cupped anteriad; Illinois and Missouri, and Rocky Mountains from Alberta to Chihuahua ..... *Austrotyla*

3b. Anterior gonopod sternum without such processes, heavily sclerotized, completely surrounding bases of coxotelopodites (Figs. 59, 61, 63); colpocoxites subequal to anterior gonopods, frequently complex and branched (Fig. 64), not cupped anteriad; Pacific Coast from central Oregon to San Francisco Bay region ..... *Taiyutyla*

4a. Anterior gonopod sternum with lateral process partially fused to lateral edge of gonopod; gonopod two-branched, mesal edge of major branch heavily laciniate (Figs. 80, 81); colpocoxite two-branched; animals without pigment, ocelli irregular; caves in northern California ..... *Plumatyla*

4b. Anterior gonopod sternum simple and bandlike (Figs. 1–7); gonopod with one or two small branches, usually not laciniated, colpocoxites with complex posterior surface (Fig. 52), but not two-branched; animals usually pigmented, ocelli round, black; eastern North America from Maine to North Carolina, Rocky Mts. of Alberta and British Columbia, Sierra Nevada Mts. of California ..... *Conotyla*

Genus *Conotyla* Cook and Collins, 1895

Craspedosoma, Bollman (in part, not of Leach, 1815), 1893, U. S. Nat. Mus. Bull. No. 46, pp. 35, 183.

Trichopetalum, McNeill (in part, not of Harger, 1872), 1887, Proc. U. S. Nat. Mus., Vol. 10, p. 330; Bull. Brookville Soc., Vol. 3, p. 8.

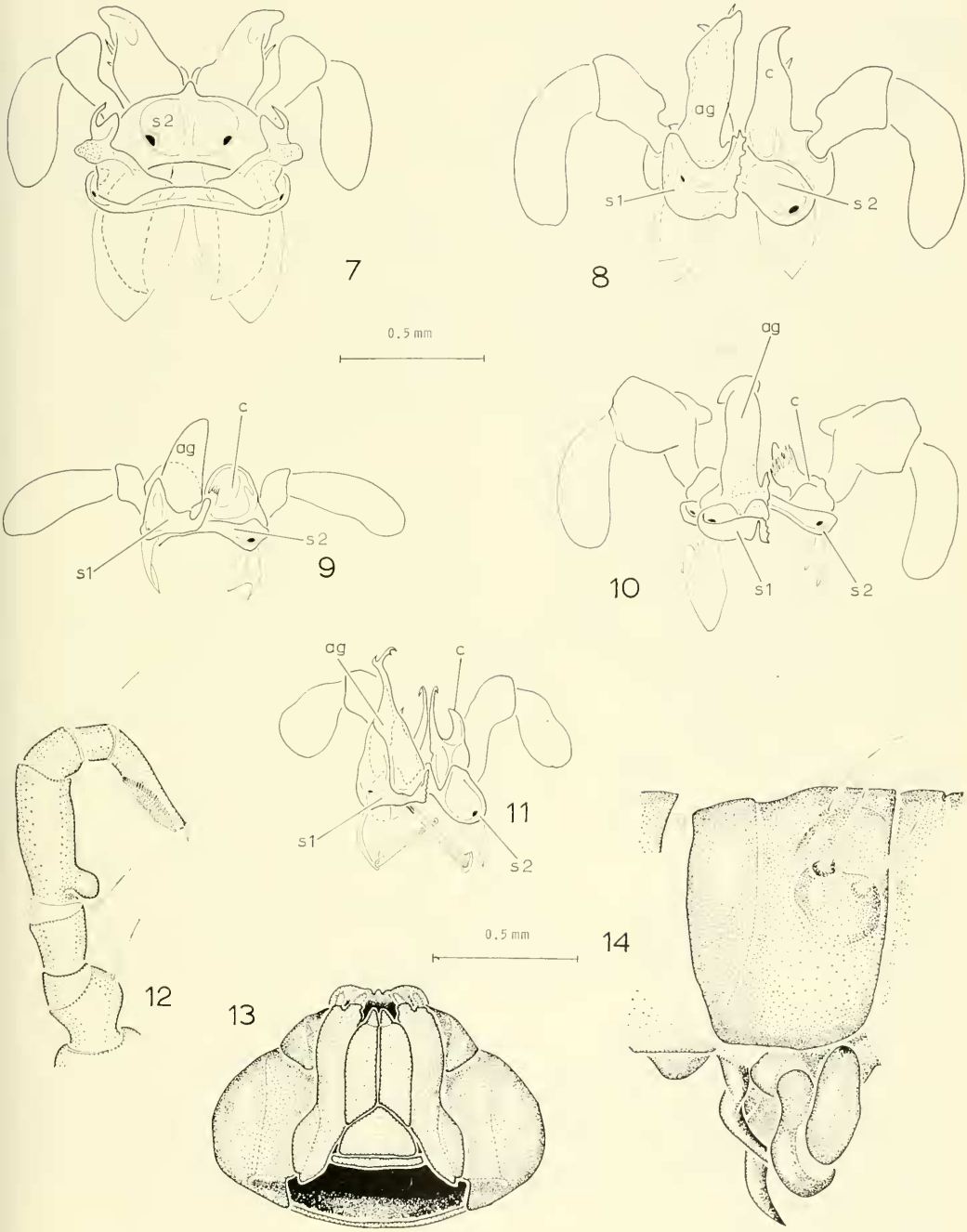
Scoterpes, Bollman (in part, not of Cope, 1872), 1893, Bull. U. S. Nat. Mus. No. 46, p. 106.

Conotyla Cook and Collins, 1895, Ann. New York Acad. Sci., Vol. 9, No. 1, pp. 70–71. Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 265.

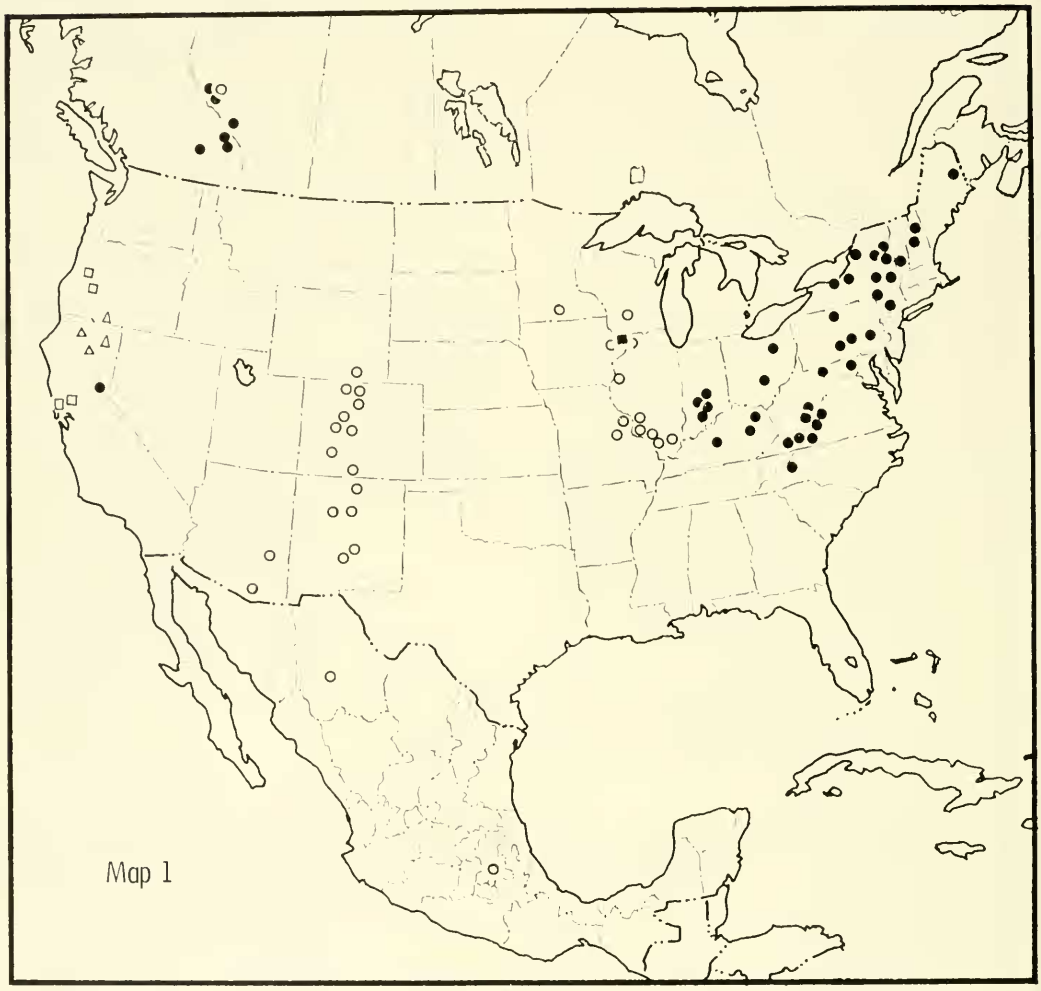
Proconotyla Verhoeff, 1932, Zool. Jahrb. Abt. Syst., Vol. 62, p. 501. NEW SYNONYMY.

Type species of *Conotyla*, *Conotyla fischeri* Cook and Collins, of *Proconotyla*, *P. blakei* Verhoeff. The generic name is a feminine Greek noun, "a cone-shaped lump," and refers to the segmental shoulders.

Diagnosis. Anterior gonopod sternum simple and bandlike, not divided. Anterior gonopods variously branched or simple and acuminate, smaller than or subequal in size to colpocoxites of posterior gonopods. Anterior gonopods usually curved posteriad of colpocoxites. Colpocoxites of posterior gonopods large, complex to simple on posterior surface. Sternum of posterior gonopods bandlike or conspicuously broadened and ovate, spiracles large and prominent, tracheal apodemes fused to sterna. Progonopodal legs of males frequently with femoral knobs, appearing on all legs in one case, and on none in another extreme. Species usually pigmented; ocelli 14–23,



Figures 7–14. Anatomy of conotylid male gonopods and of *Conotyla blakei*. Fig. 7. *Conotyla albertana* gonopods, anterior view. Fig. 8. *Taiyutyla carvallis* gonopods, anterior view. Fig. 9. *Austrotyla coloradensis* gonopods, anterior view. Fig. 10. *Achemenides pectinatus* gonopods, anterior view. Fig. 11. *Plumatyla humerosa* gonopods, anterior view. Figs. 12–14. *Conotyla blakei*. Fig. 12. Leg 7, posterior view. Fig. 13. Gnathochilarium, ventral view. Fig. 14. Segment 7 of male, lateral view (anterior to the left).



Map 1. North America, showing distribution of conotylid genera (some records of immature specimens included); dots, *Conotyla* spp.; circles, *Austrotyla* spp.; triangles, *Plumatyla* spp.; solid square, *Achemenides pectinatus;* open squares, *Taiyutyla* spp.

usually round, black, arranged in triangular eyepatch in four or five rows. Coxae of tenth legs with large coxal glands, not lobed; coxae of eleventh legs normal; prefemur of eleventh legs with prominent posterior hooks.

Species. Fifteen known.

Distribution. See Map 1. Eastern North America from Maine through Vermont, New Hampshire and New York to Ohio and Indiana in the west and to North Carolina in the east; center of diversity is apparently in eastern West Virginia and southwestern Virginia; Rocky Mountains of the Alberta-British Columbia border; Sierra Nevada Mts. of California.

Key to Species (Males)

1a. Pregonopodal legs only slightly more crassate than postgonopodal legs, without knobs; Nevada Co., California ..... *extorris*

1b. Pregonopodal legs strongly crassate (Fig.

12), at least leg 4 or 7 with a femoral knob 2
2a. Leg 4 with a femoral knob 3
2b. Leg 4 without a femoral knob, leg 7 with strong femoral knob (Fig. 12); Vermont, New York, Pennsylvania, Maryland, and West Virginia, often in caves ..... *blakei*
3a. Leg 7 without a femoral knob 4
3b. Leg 7 with a strong femoral knob 6
4a. Legs 2 and 3 with femoral knobs; Virginia ..... *celeno*
4b. Legs 2 and 3 without femoral knobs 5
5a. Leg 5 without a femoral knob; Indiana ..... *bollmani*
5b. Leg 5 with a femoral knob; Virginia ..... *venetia*
6a. Leg 6 without a femoral knob; British Columbia ..... *atrolineata*
6b. Leg 6 with a femoral knob 7
7a. Leg 2 with a femoral knob 8
7b. Leg 2 without a femoral knob 9
8a. Leg 1 with a femoral knob; West Virginia ..... *vista*
8b. Leg 1 without a femoral knob; Virginia ..... *melinda*
9a. Leg 3 with a strong femoral knob 10
9b. Leg 3 with a weak femoral knob, or lacking a knob 11
10a. Posterior surface of colpocoxite (Fig. 52) with several branches; Alberta ..... *albertana*
10b. Posterior surface of colpocoxite (Fig. 29) with a single plumose branch; Kentucky ..... *elpenor*
11a. Leg 3 with a weak femoral knob 12
11b. Leg 3 without a femoral knob 13
12a. Colpocoxite (Fig. 38) with an attenuate apical hook; Virginia ..... *aeto*
12b. Colpocoxite (Fig. 31) blunt apically; West Virginia ..... *smilax*
13a. Femoral knob of leg 4 weakly developed; Ohio ..... *personata*
13b. Femoral knob of leg 4 strong 14
14a. Colpocoxite (Fig. 36) with an attenuate distal process; Ohio ..... *ocypetes*
14b. Colpocoxite (Fig. 25) apically blunt; New York ..... *fischeri*

The following arrangement into species groups is not wholly a natural one, but serves the purpose of making the task of writing abbreviated species diagnoses easier. The arrangement is based primarily on the form of the anterior gonopods.

The *Blakei* Group

This group is characterized by simple, usually acuminate anterior gonopods in which the anterior branch is reduced to a poorly sclerotized plumose rod (Figs. 4, 19, 22). *Conotyla blakei* and *C. bollmani* are clearly related, but the resemblance of *C. extorris* to these species is probably a result of parallelism.

Conotyla blakei (Verhoeff) Figures 12–18

Proconotyla blakei Verhoeff, 1932, Zool. Jahrb. Abt. Syst., Vol. 62, p. 501, figs. 33–37. Hoffman and Chamberlin, 1958, U. S. Nat. Mus. Bull. 212, p. 101. Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 271.

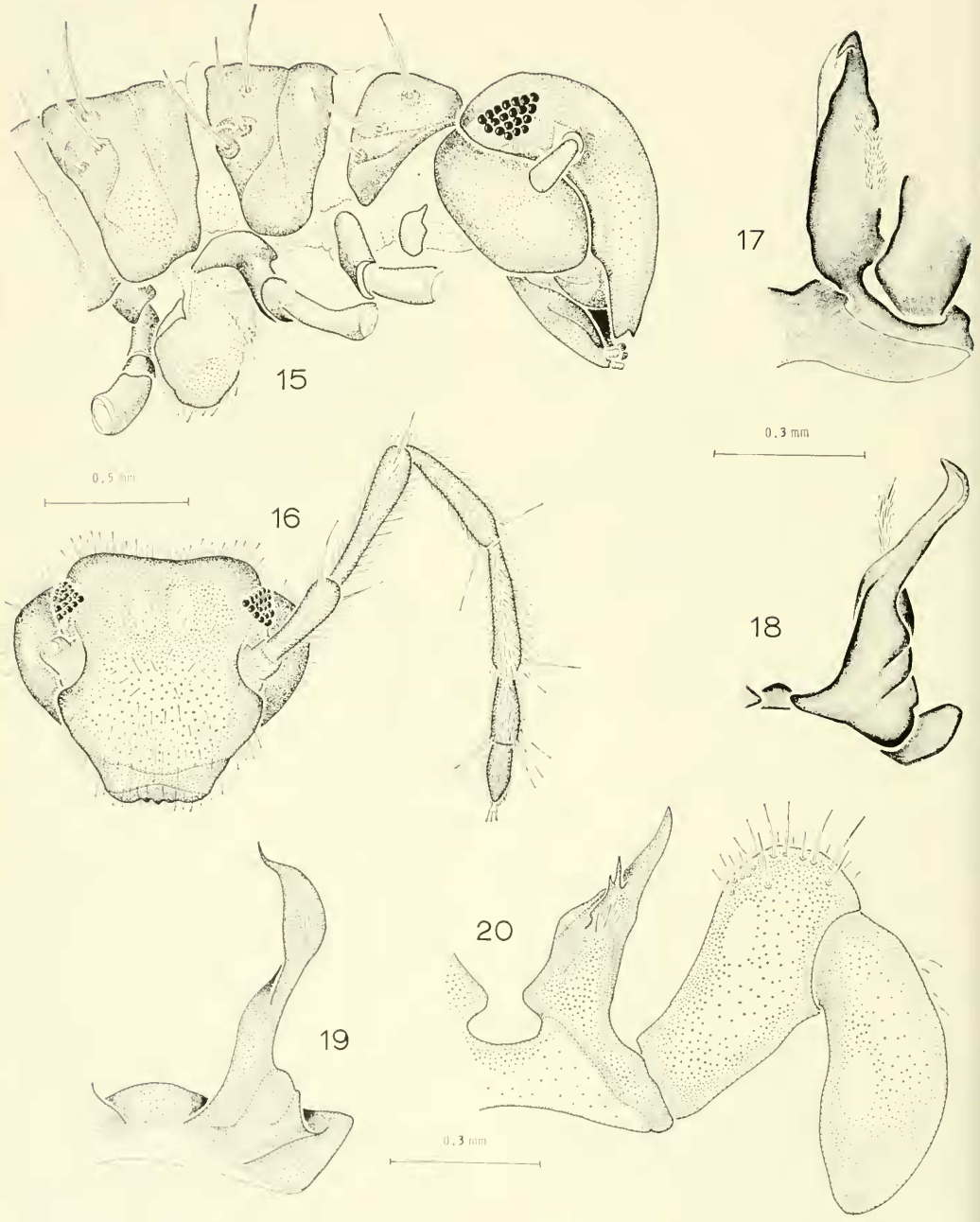
Conotyla vaga Loomis, 1939, Bull. Mus. Comp. Zool., Vol. 86, pp. 182–183, fig. 10. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 99. NEW SYNONYMY.

Types. Male holotype of *P. blakei*, Mt. Adams, Essex Co., N. Y., whereabouts unknown; of *C. vaga*, South Temple Cave, Berks Co., Pennsylvania; in the M. C. Z., examined.

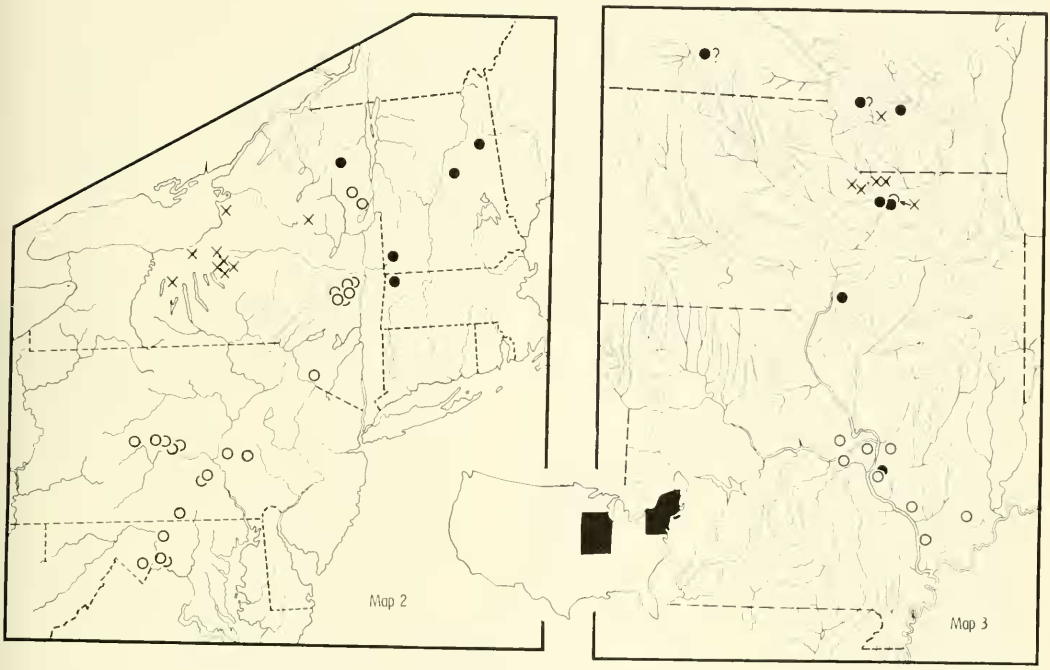
Diagnosis. Distinct from other species of the *blakei* group in having an apophysis on leg 7 (Fig. 12); *bollmani* has an apophysis only on leg 4, and *extorris*, besides occurring in California, has no pregonopodal leg modifications at all.

Description of male from Mt. Equinox, Bennington Co., Vermont. Length, 18.0 mm. Eyepatches (Figs. 15, 16) triangular, 18 ocelli in 4 rows on both sides. Antennal articles (Fig. 16) in order of length: 3, 5, 4, 2 = 6, 7, 1. Leg 7 (Fig. 12) with large, capitate, proximal apophysis on femur, pregonopodal legs otherwise unmodified. Anterior gonopods (Fig. 18) prolonged directly into posterior branch, anterior branch single, inconspicuous plumose rod; posterior branch narrowing at tip, curving around lateral side of colpocoxites of posterior gonopods. Colpocoxites of posterior gonopods (Fig. 17) acuminate, drawn out smoothly into decurved terminal process; just below origin of terminal process is a mesal transparent plate; pilose area limited to lateral surface, without branches; mesal tooth and lateral notch not present.

Remarks. This species is widely distributed (Map 2). It has been collected



Figures 15–20. Anatomy of *Conotyla blakei* and gonopods of *Conotyla* spp. Figs. 15–18. *Conotyla blakei*. Fig. 15. Head and anterior trunk segments of female, lateral view. Fig. 16. Head of female, anterior view. Fig. 17. Colpocoxite of left posterior gonopod, posterior view. Fig. 18. Left anterior gonopod of male, posterior view. Figs. 19–20. *C. bollmani*. Fig. 19. Left anterior gonopod of male, posterior view. Fig. 20. Left posterior gonopod, posterior view.



Map 2. Part of northeastern United States, showing distribution of some *Conotyla* spp.; dots, epigean records of *C. blakei*; circles, cave records of *C. blakei*; crosses, records of *C. fischeri*. Question mark indicates a dubious identification.
Map 3. Part of central United States, showing distribution of *Austrotyla* and *Achemenides*; dots, epigean records of *Austratyla specus*; circles, cave records of *A. specus*; crosses, records of *Achemenides pectinatus* (all cave records). Question mark indicates a dubious identification.

in the Adirondack counties of New York in Canadian Zone Forests and in caves; in caves in Sullivan, Orange, and Schoharie counties, and in numerous caves in central Pennsylvania and Maryland, and a single case in Jefferson Co., West Virginia. I have personally collected *blakei* in a scrubby fir forest at 3800 feet on the summit of Big Equinox Mountain, Bennington Co., Vermont, where it was abundant under the bark of both standing and fallen dead trees. The distribution of *blakei* follows exposures of limestone and marble up to the Adirondacks, where it is also found on other substrates. This distributional pattern seems to clearly indicate that *blakei* followed the boreal forests north with the retreat of the Wisconsin ice at the end of the Pleistocene, leaving behind relict populations in suitable habitats, such as limestone caves.

The cave populations described by Loomis (1939) as *vaga* differ hardly at all from the typical form of *blakei*, except that the pigmentation is much weaker in some specimens and the arrangement and size of the ocelli is somewhat irregular.

Conotyla bollmani (McNeill)
Figures 19, 20

Trichopetalum bollmani McNeill, 1887, Proc. U. S. Nat. Mus., Vol. 10, p. 330.

Scotherpes wyandotte Bollman, 1889, Proc. U. S. Nat. Mus., Vol. 11, p. 405. Misspelling of *Scoterpes wyandotte*. NEW SYNONYMY.

Conotyla bollmani, Cook and Collins, 1895, Ann. New York Acad. Sci., Vol. 9, p. 76, figs. 79–94. Loomis, 1943, Bull. Mus. Comp. Zool., Vol. 92, p. 381 (key). Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 98 (list).

Conotyla wyandotte, Cook and Collins, 1895, Ann. New York Acad. Sci., Vol. 9, p. 78, fig. 101; Chamberlin and Hoffman, 1958, U. S. Nat.

Mus. Bull. 212, p. 100 (list). NEW SYNONYMY.

Types. Male types of *T. bollmani* from Mayfield's Cave, Bloomington, Monroe Co., Indiana; type in U. S. National Museum (?); of *C. wyandotte*, near Wyandotte cave, Crawford Co., Ind.; type in U. S. National Museum.

Diagnosis. Differs from the other species of the *blakei* group in having an apophysis on the fourth article of the fourth leg; *blakei* and *extorris* both lack such an apophysis.

Description of male from Boone Cave, Owen Co., Indiana. Length, 14.0 mm. Ocelli 22 in four rows plus single ocellus on the right side, 20 ocelli in four rows on left side. Antennal articles in order of length, 3, 4, 5, 2, 6, 7, 1. Body white, ocelli somewhat irregular in shape and arrangement. Leg 4 with large capitate apophysis on femur. Anterior gonopods (Fig. 19) simple, acuminate to tip of posterior branch, anterior branch a simple, inconspicuous plumose rod; lateral shoulder low, rugose. Anterior gonopods passing around lateral side of colpocoxites of posterior gonopods *in situ*. Colpocoxites of posterior gonopods (Fig. 20) bluntly pointed, without definite terminal process; mesal tooth bifid; pilose area small, restricted to part of posterior surface.

Notes. Known primarily from caves and a few surface records in south-central Indiana. Surface specimens are normally pigmented, while cave populations are usually white and have rather irregular ocelli. The identity of immature and female specimens from adjacent regions of Kentucky is unclear. Map 7 shows the boundaries of the supposed glacial maxima of Wisconsin and of Illinois time (from Wayne and Zumberge, 1965), but since the availability of a suitable substrate also affects the distribution of cave animals, and surface records are scarce, I would rather not speculate on the possible history of this species.

Conotyla extorris n. sp.
Figures 22, 23

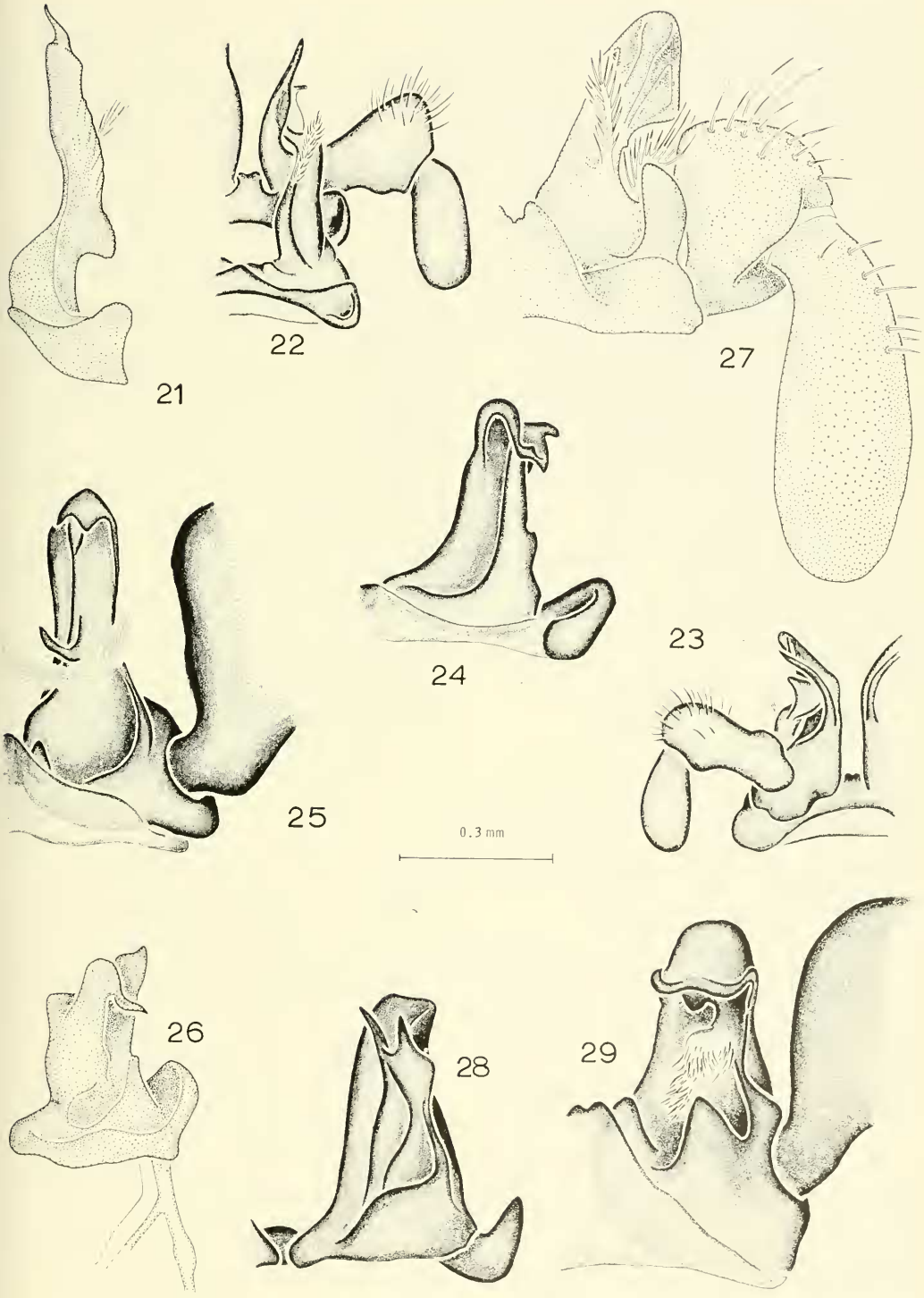
Type. Male holotype from 1 mile south of Grass Valley, Nevada Co., California, collected January 5, 1968, by D. E. Bragg and R. F. Denno. The specific epithet is a Latin adjective meaning "banished, exiled," and refers to the distance separating this species from the others of its genus.

Diagnosis. Distinct from others of the *blakei* group in having no modifications at all on the pregonopodal legs, which are of normal size and lacking apophyses. The gonopods (Figs. 22, 23) are only about a third the size of those of *bollmani* and *blakei*.

Description of holotype male. Length, 12.6 mm, the smallest known species of *Conotyla*. Eyepatches triangular, 20 ocelli in four rows on the right side, 19 ocelli in four rows on the left side. Antennal joints in order of length: 3, 5, 4, 6, 2, 7, 1. Pregonopodal legs unmodified. Anterior gonopods (Fig. 22) with posterior branch large, broadened near the tip and recurved, passing laterad of the colpocoxites of the posterior gonopods; anterior branch a single, inconspicuous plumose rod. Colpocoxites of the posterior gonopods (Fig. 23) with terminal process sharply curved dorsad and slightly laterad; mesal tooth (?) a long rod reaching to the tip of the colpocoxite; lateral notch and pilose area absent.

→

Figures 21–29. Male gonopods of *Conotyla* spp. Fig. 21. *Conotyla bollmani*, left anterior gonopod, lateral view. Figs. 22–23. *C. extorris*. Fig. 22. Right gonopods, anterior view. Fig. 23. Right gonopods, posterior view. Figs. 24–25. *C. fischeri*. Fig. 24. Left anterior gonopod, posterior view. Fig. 25. Left posterior gonopod colpocoxite, posterior view. Figs. 26–27. *C. personota*. Fig. 26. Left anterior gonopod, posterior view. Figs. 28–29. *C. elpenor*. Fig. 28. Left anterior gonopod, posterior view. Fig. 29. Colpocoxite of left posterior gonopod, posterior view.


21
22
27
24
23
25
0.3 mm
26
28
29

Notes. The type locality (Map 6) is near the Boyce Thompson Institute of Forest Studies, at about 2400 ft. elevation. The area is forested primarily with pine, *Arctostaphylos*, and oaks. Michael Gardner (personal communication) has recorded the millipeds *Brachycybe producta*, *Wamokia sierra*, *Buzonium crassipes*, and *Placerna dorada*, among others, from Grass Valley.

The assignment of this species to *Conotyla* may prove to be controversial. It has many of the characters of *Taiyutyla*, a genus geographically closer. However, the form of the gonopods and especially the anterior gonopod sternum favor the present placement. If more new species with a similar combination of characters are collected, a new genus may be justified.

The *Fischeri* Group

This is a compact, closely related group of three species from New York, Ohio, and Kentucky, characterized by the reduction of the anterior branch of the anterior gonopods, and by their similar colpocoxites.

Conotyla fischeri Cook and Collins
Figures 3, 24, 25

Conotyla fischeri Cook and Collins, 1895, Ann. New York Acad. Sci., Vol. 9, pp. 71–74, figs. 55–78. Loomis, 1943, Bull. Mus. Comp. Zool., Vol. 92, p. 382 (key). Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 82, pp. 265–266, fig. 7. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, pp. 98–99 (list).

Types. None designated by original authors; type locality restricted by Chamberlin and Hoffman (1958) to Syracuse, Onondaga Co., New York.

Diagnosis. Distinct in the form of the gonopods from all other species except the closely related *personata;* differing from *personata* in the gonopods as described under that species, and also in having a much more pronounced apophysis on the femur of leg 4.

Description of male from Skaneateles, Onondaga Co., New York. Length, 19.4 mm. Eyepatches triangular, 20 ocelli in four rows on left side, 21 ocelli in four rows on right side. Antennal segments in order of length: 3, 4 = 5, 2, 6, 7, 1. Pregonopodal legs somewhat less enlarged than usual, legs 4–7 usually with apophyses on femur; distal on leg 4, mesal on legs 5 and 6; large, proximal and toothed, if present, on leg 7, but not resting on anterior gonopod *in situ.* Anterior gonopods (Fig. 24) short, subquadrate, posterior branch absent, anterior branch short, not curving around colpocoxites of posterior gonopods; lateral shoulder poorly developed. Colpocoxites of posterior gonopods (Fig. 25) without a terminal process, but with a prominent ridge on the posterior surface, bearing near its proximal end a long, rather flattened rod; lateral notch absent; pilose area with one or two pilose branches.

Notes. Cook and Collins (1895) had over 100 specimens from Onondaga, Ontario, and Wayne counties, New York (Map 2). They were collected primarily from rotting litter in woods, and under the moist, rotting bark of fallen trees. Hoffman (1961) reported the species from Hamilton Co., 2 miles west of Morehouseville, but gave no additional ecological data. His material, which I re-examined for this study, differs from the Cook and Collins series and from other Onondaga Co. specimens in having the apophysis of the seventh legs very small, or absent; the other apophyses are normally developed. The species is evidently limited to the rolling hills south and east of Lake Ontario (Map 2), but extension of its range into areas bordering on Lake Erie would be most interesting, as it might indicate the exact nature of this species' relationship to *personata*, which occurs in similar terrain just south of Lake Erie in Ohio. Several intriguing immature specimens from Ontario, northern New York, and from Potter Co., Pennsylvania, this latter locality near the southern limit of Pleistocene glaciation, may belong to this species.

Conotyla personata n. sp.
Figures 26, 27

Type. Holotype male collected by A. A. Weaver, May 5, 1960, Funk's Hollow, Wooster, Wayne Co., Ohio. The specific epithet is a Latin adjective, meaning "masked, hidden," and refers to my original confusion between this species and *fischeri.*

Diagnosis. Very similar to *fischeri,* but distinct in details of the gonopods. The lateral shoulder of the anterior gonopod is much higher (Fig. 26) than in *fischeri,* and the posterior branch is longer and more pronounced; the lateral notch of the colpocoxite is almost obsolete in *fischeri;* in *personata* it is the deepest and broadest of any species in the genus.

Description of male holotype. Length, 14 mm. Ocelli in four irregular rows on each side, 21 on right side and 23 on left side. Antennal segments in order of length: 3, 4, 5, 6 = 2, 7, 1. Fourth joints of legs 4, 5, and 6 with small, distal knob; fourth joint of leg 7 with long, apically toothed proximal process that *in situ* rests on the lateral shoulder of anterior gonopod. Sternum of anterior gonopods as described for genus, but lateral edge not visible in posterior view. Anterior gonopods (Fig. 26) short, subrectangular in posterior view; lateral shoulder prominent; anterior branch absent, posterior branch curved dorsad slightly. Colpocoxite of posterior gonopod (Fig. 27) bluntly subtriangular, all processes and teeth undeveloped; pilose area extended into at least one pilose branch; lateral notch deep, extending nearly halfway up colpocoxite.

Notes. The male holotype was taken in a deep, heavily wooded, mesic ravine surrounded by rolling cultivated land. The north-facing slope of the ravine supports a heavy mixed forest with much hemlock; the south-facing slope is forested with oak and pine. A study of the humus fauna of these slopes produced several immature and female *Conotyla* in early fall. This species is possibly widespread in northern and central Ohio, but the only males are from the type locality, and nearby.

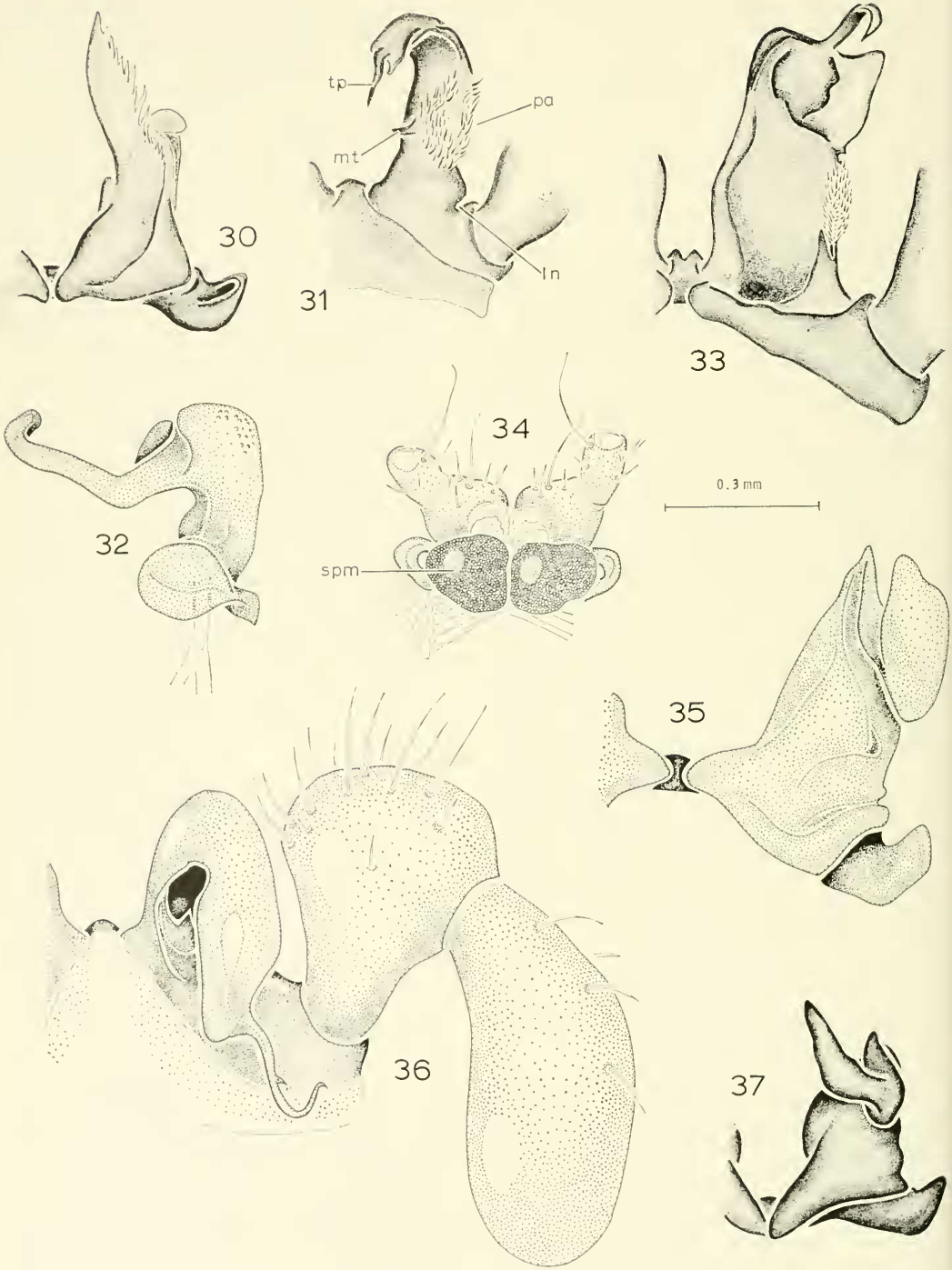
Conotyla elpenor n. sp.
Figures 28, 29

Type. Male holotype collected with another male and two females on 26 February 1966 by Branley A. Branson, nine miles northwest of Pine Ridge, elevation 800 ft. (250 m), Wolfe County, Kentucky. The specific epithet refers to one of the companions of Odysseus, changed into a swine by Circe's witchcraft.

Diagnosis. With the characters of the *fischeri* group; distinct in the form of the anterior gonopods, with two well-defined branches (Fig. 28), and in the colpocoxites of the posterior gonopods having an exceptionally deep lateral notch and coxal pocket.

Description of holotype male. Length, 18 mm. Eyepatches subtriangular, 20 ocelli in four rows on each side. Antennal articles in order of length: 3, 4 = 5, 6, 2, 7, 1. Pregonopodal legs 3 through 7 with apophyses on femur; apophysis of leg 3 small, distal; of legs 4 and 5 mesodistal, larger; of leg 6, proximal and blunt, of leg 7 proximal and greatly elongated, coarsely toothed distally, resting *in situ* posterior of lateral shoulder of anterior gonopod. Anterior gonopod (Fig. 28) with lateral shoulder, large, lamellate; two branches of gonopod may represent a bifurcation of the posterior branch, *in situ* they extend laterally around colpocoxites of posterior gonopods. Colpocoxites of posterior gonopods (Fig. 29) closely resembling those of *personata;* but somewhat longer, bent sharply posteriad, blunt; lateral notch deep, pilose area with two indistinct branches.

Notes. The holotype and the other known specimens were taken from beneath a rotting log in mixed hardwood forest. Though the specimens were labelled as being from Wolfe Co., the distance north-


30
tp
pa
mt
ln
31
33
34
0.3 mm
32
spm
35
36
37

west of Pine Ridge indicated on the label would place the locality in Powell Co. This species is known only from the type locality. A female from Carter Co., Kentucky (MCZ), may belong to *elpenor* (Map 5).

The *Smilax* Group

The single species of this group, *C. smilax*, is unique in several ways, but may be related to the preceding group.

Conotyla smilax n. sp.
Figures 30, 31

Type. Holotype male collected ca. elev. 3000 ft. (1000 m), Kate's Mt., above White Sulphur Springs, Greenbriar Co., West Virginia, April 1, 1967, by W. A. Shear. The specific epithet is a Latin noun in apposition and refers to *Smilax*, the greenbriar, abundant at the type locality.

Diagnosis. Distinct from all other related species of *Conotyla* in lacking the posterior branch of the anterior gonopods (Fig. 30). The anterior branch is well developed and had a deeply laciniated membrane running the length of its posterolateral edge.

Description of male holotype. Length, 13.3 mm. Ocelli in four rows on each side, 20 ocelli in each eyepatch. Legs 3 through 7 enlarged and crassate, knob present on femur of legs 3 through 7. Antennal articles in order of length: 3, 4 = 5, 6 = 2, 7, 1. Sternum of anterior gonopods as described for genus. Anterior gonopods (Fig. 30) with conspicuous lateral shoulder, but knob of fourth segment of leg 7 does not rest on shoulder when gonopod is *in situ;* posterior branch absent, anterior branch large, thin, nearly half as long as remainder of coxotelopodite, extending straight ventrad, with a deeply laciniated membrane on posterolateral surface. Colpocoxites of posterior gonopods with terminal process long, aciculate; mesal tooth inconspicuous, pilose area with definite branches, extensive (Fig. 31).

Notes. The male holotype, the only known specimen, was collected after a light rain, crawling about on dead twigs under a *Rhododendron.* The type locality (Map 5) is an unusual area, dissected into adjacent areas of very mesic forest of mixed hardwoods and hemlock and "shale barrens," with a hot, dry microclimate and sparse vegetation of scrub oak and Virginia pine. *Apheloria trimaculata* and *Cleidogona major* were taken in abundance.

The *Venetia* Group

These species have similar anterior gonopods in which the anterior branch is absent and the posterior branch long, giving a right-angled appearance to the gonopod (Fig. 33).

Conotyla venetia Hoffman
Figures 32–34

Conotyla venetia Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 267, Pl. IX, figs. 1–3.

Type. Male holotype from three miles north of Clifton Forge, Alleghany Co., Virginia; type in U. S. National Museum, examined.

Diagnosis. Distinct from all other species of *Conotyla* in bearing apophyses on the fourth article of legs 4 and 5 only; distinct in details of the gonopods from others of the *venetia* group.

Description of male from Warm Spring Mt., Alleghany Co., Virginia. Length, 14.5 mm. Ocelli 20 on each side, in four rows. Antennal segments in order of length: 3, 4, 5, 2, 6, 7, 1. Legs 4 and 5 with small

←

Figures 30–37. Male gonopods of *Conotyla* spp. Figs. 30–31. *Conotyla smilax.* Fig. 30. Left anterior gonopod, posterior view. Fig. 31. Left posterior gonopod, posterior view. Figs. 32–34. *C. venetia.* Fig. 32. Left anterior gonopod, lateral view. Fig. 33. Colpocoxite of left posterior gonopod, posterior view. Fig. 34. Coxae of 10th legs of male, ventral view. Figs. 35–36. *C. ocypetes.* Fig. 35. Left anterior gonopod, posterior view. Fig. 36. Left posterior gonopod, posterior view. Fig. 37. *C. aeto,* left anterior gonopod, posterior view.

apophyses on femora, distal in position. Anterior gonopods (Figs. 32, 33) with posterior branch extending at right angle posteriad from telopodite, anterior branch absent; lateral shoulder well developed, heavily rugose on lateral surface; posterior branch extending *in situ* well around lateral surface of colpocoxite of posterior gonopod. Colpocoxite of posterior gonopod (Fig. 34) subrectangular in outline; terminal process definitely set off by prominent shoulders at its base; mesal tooth reduced to small knob; pilose area lateral; lateral notch present, but small.

Notes. This species is known only from two localities in Alleghany Co., Virginia (Map 5), separated by nearly 3000 ft. (1000 m) of altitude (400–3400 ft.). Hoffman (1961) implies that the species may be widespread in central western Virginia.

Conotyla ocypetes n. sp.
Figures 35, 36

Type. Male holotype from Sugar Grove, Fairfield Co., Ohio, collected by J. H. Emerton, December 26, 1915. The specific epithet is a noun in apposition, the Greek name of one of the three Harpies of mythology.

Diagnosis. Distinct from others of the *venetia* group in details of the gonopods and in the apophyses of the pregonopodal legs; from *aeto* in having a strong apophysis on the third joint of leg 2 and none on leg 3, and from *venetia* by having apophyses on legs 6 and 7.

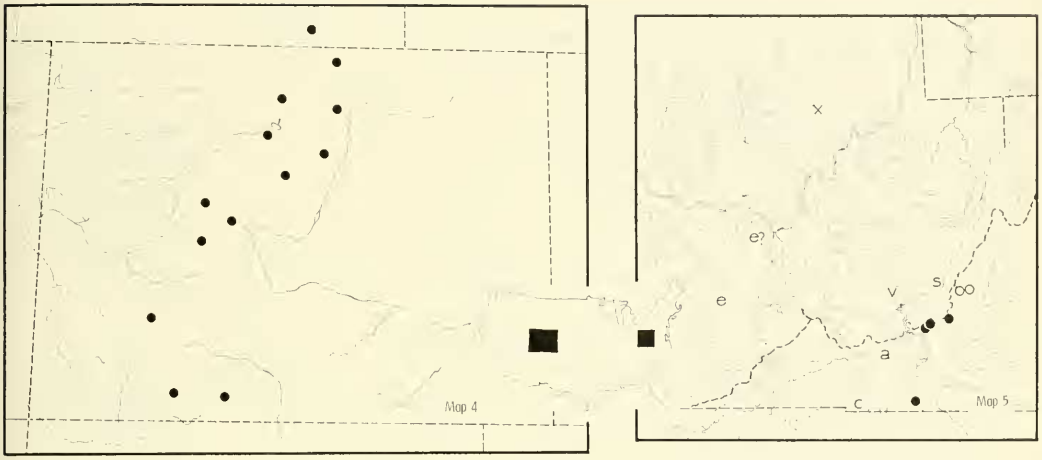
Description of holotype male. Length, 20.0 mm. Eyepatch of right side triangular-truncate, 20 ocelli in four rows; eyepatch of left side probably anomalous, five large ocelli in two rows. Antennae missing. Leg 2 with strong distal apophysis on third joint; legs 4 through 6 with apophyses on femora becoming smaller and mesal; leg 7 with small proximal apophysis on femur that does not touch anterior gonopod *in situ*. Anterior gonopod (Fig. 35) typical of *venetia* group, anterior branch absent, posterior branch large, becoming spatulate distally, curving around lateral side of colpocoxites of posterior gonopods; lateral shoulder not at all developed, instead gonopod is highly ridged mesally. Colpocoxites of posterior gonopods (Fig. 36) unusually long, but arched dorsad; terminal process very long and irregularly sinuate, with a small triangular tooth about half its length from the origin; mesal tooth present; lateral notch absent; pilose area small, limited to lateral margin.

Notes. The male holotype was collected with a female and an immature specimen; probably all are of the same species. The southern section of Fairfield County (Map 5) is in the valley of the Hocking River, a region of low hills highly dissected into deep gorges with abrupt sandstone walls. Most of these gorges are very moist; the vegetation is mostly hemlock and beech. Emerton unfortunately failed to indicate exactly where the type specimen was obtained, but it seems likely that such a gorge as the ones described above would provide the most favorable habitat. However, several years of extensive collecting in the Hocking area by Dr. A. A. Weaver and others has resulted in the collection of no conotylids.

Conotyla aeto n. sp.
Figures 37, 38

Type. Male holotype from top of Clinch Mt., ca. 4500 ft. (1500 m), Burke's Garden, Tazewell Co., Virginia, collected November 14, 1965, by Radford College Biology Club. The specific epithet, like *celeno* and *ocypetes*, is a Greek noun in apposition, the name of one of the Harpies of mythology.

Diagnosis. Distinct from other species of the *venetia* group in the modifications of the pregonopodal legs and in details of the gonopods; from *venetia* in having apophyses on legs 6 and 7, and from *ocypetes* in having a slight apophysis on leg 3 and none on leg 2.



Map 4. Colorado, dots showing distribution of *Austrotyla coloradensis*.
Map 5. North central Appalachian region and part of Ohio, showing distribution of *Conotyla* spp.; dots, *C. melinda*; circles, *C. venetia*; cross, *C. ocypetes*; a, *C. aeto*; c, *C. celeno*; e, *C. elpenor*; v, *C. vista*; s, *C. smilax*. Question mark indicates a dubious identification.

Description of holotype male. Length, 15 mm. Eyepatch triangular, 21 ocelli in four rows and single ocellus on right side; 20 ocelli with same arrangement on left side. Antennal articles in order of length: 3, 4, 5, 2 = 6, 7, 1. Legs 3 through 7 with apophyses on femora, that of leg 3 small, becoming stronger to leg 6, all distal in position; apophysis of leg 7 proximal in position, capitate and toothed, but not resting on shoulder of anterior gonopod *in situ*. Prefemoral hooks of leg 11 particularly large. Anterior gonopods (Fig. 37) typical of *venetia* group, anterior branch absent, posterior branch large, broadened towards tip, extending well around lateral side of colpocoxites of posterior gonopods in undissected animal; lateral shoulder poorly developed. Colpocoxites of posterior gonopods (Fig. 38) distinct; terminal process flattened dorsoventrally, hooked dorsad; subterminal process expanded laterad into a large plate that in natural position covers apical end of posterior branch of anterior gonopod and is heavily ridged on posterior side, the distal ends of the ridges drawn out into prominent teeth (Fig. 38); mesal tooth absent; pilose area with single pilose branch; lateral notch absent.

Notes. The northeastern part of Clinch Mountain, which extends from southwest to northeast across western Virginia, forms the southern and western wall of Burke's Garden, an unusual semicircular anticlinal valley, the floor of which is at nearly 3000 ft. (1000 m) elevation, surrounded by mountains up to 4800 ft. (1600 m), with their tops in well-developed Canadian Zone forests.

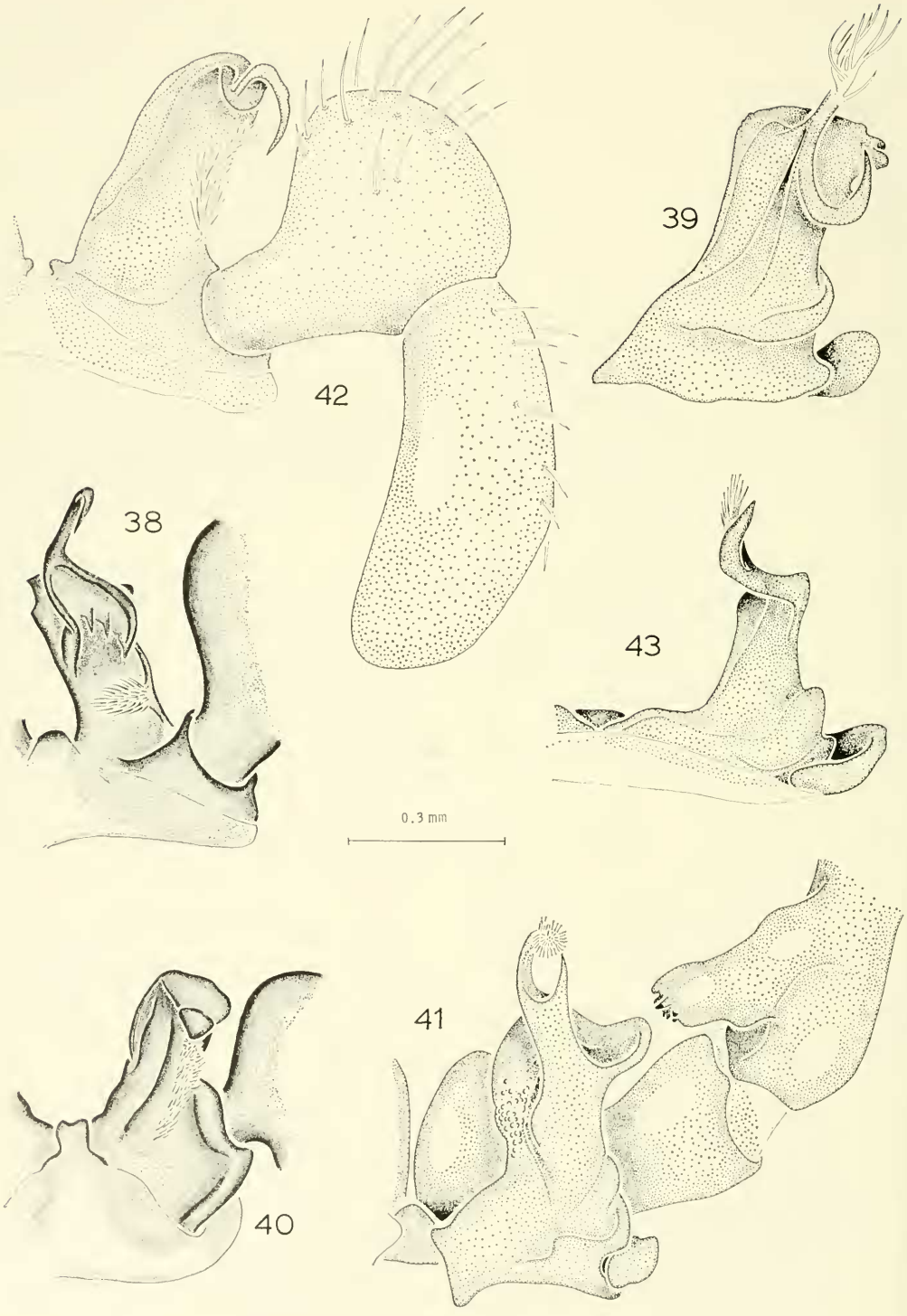
The *Melinda* Group

Both branches of the anterior gonopod are nearly equal in this group. The posterior branch is distally plumose, but strong and heavy.

Conotyla melinda Hoffman
Figures 1, 2, 39, 40

Conotyla melinda Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 266, Pl. IX, figs. 4–6.

Type. Male holotype from Brush Mt., 2 miles west of Blacksburg, Montgomery Co., Virginia; type in U. S. National Museum, examined.


42
39
38
43
0.3 mm
40
41

Diagnosis. Distinct from others of the *melinda* group in details of the gonopods and the distribution of apophyses on the pregonopodal legs; *vista* has apophyses on all the pregonopodal legs, *celeno* lacks them on leg 6.

Description of male from type locality. Length, 18.5 mm. Ocelli 20 in triangular eyepatch of four rows on right side, 19 ocelli in four rows on left side. Antennal articles in order of length: 3, 5, 4, 2, 6, 7, 1. Leg 2 with large apophysis on third joint; legs 3 through 6 with similar apophyses on femora, largest on legs 4 and 5, distal in position. Anterior gonopods (Fig. 39) with anterior branch larger than posterior, twisted and deeply laciniate at the end; posterior branch a short hook; lateral shoulder with prominent knobs. Colpocoxites (Fig. 40) of posterior gonopods with terminal process bluntly triangular, curved posteriad, pilose area extensive; mesal tooth absent, lateral notch inconspicuous.

Notes. Hoffman's original description overlooked the posterior branch of the anterior gonopod. Reported from Craig, Montgomery, Giles and Patrick counties in southwest Virginia (Map 5). All records are for November and December, except for a pair taken *in copula* on March 15, 1956, in oak woods. Other records are from *Rhododendron* thickets and a sinkhole (Hoffman, 1961).

Conotyla vista n. sp.
Figures 41, 42

Type. Male holotype collected by W. A. Shear and David Bard, January 25, 1967, Natural Tunnel No. 1, Grandview State Park, 13 miles northeast of Beckley, Raleigh Co., West Virginia, elevation 2250 ft. (710 m). The specific epithet is a Latin noun in apposition and refers to the sweeping view of the New River canyon visible from the type locality.

Diagnosis. Distinct from the other species of the *melinda* group, and from all other known *Conotyla* species, in having prominent apophyses on all the pregonopodal legs, including the first.

Description of holotype male. Length, 26 mm, the largest known species of the family. Nineteen ocelli in four rows in a triangular eyepatch on left side, 16 ocelli in four rows on right side. Antennal joints in order of length: 3, 4, 5, 2, 6, 7, 1. Joint 3 of legs 1 and 2 with mesal apophyses of moderate size; similar apophyses on the femora of legs 3 through 6, becoming largest on leg 4; femur of leg 7 with an exceptionally large, apically toothed, sinuate process on proximal end, that *in situ* rests in pocket, on anterior gonopod of each side (Fig. 41). Anterior gonopods with lateral shoulder prominent and rimmed; mesal to shoulder apical region of gonopod is depressed, forming a pocket in which apophysis of leg 7 fits when gonopods are *in situ;* posterior branch somewhat larger than anterior, somewhat laciniate apically, both branches pass laterally around the colpocoxites *in situ.* Colpocoxites of posterior gonopods (Fig. 42) with a long, sigmoid and aciculate apical process, pilose area occupying the lateral margin; lateral notch and mesal tooth absent. Colpocoxite distinctly thickened on mesal margin.

Notes. The male holotype is the only known specimen. The type locality (Map 5) is a ridge of heavily faulted, coarse sandstone overlooking the 1200 foot deep gorge of the New River. The Natural Tunnels are roofed crevices formed by down-

←

Figures 38–43. Male gonopods of *Conotyla* spp. Fig. 38. *Conotyla aeta*, colpocoxite of left posterior gonopod, posterior view. Figs. 39–40. *C. melinda.* Fig. 39. Left anterior gonopod, posterior view. Fig. 40. Colpocoxite of left posterior gonopod, posterior view. Figs. 41–42. *C. vista.* Fig. 41. Left anterior gonopod and basal segments of leg 7, posterior view. Fig. 42. Left posterior gonopod, posterior view. Fig. 43. *C. celeno*, left anterior gonopod, posterior view.

slope creeping of sandstone blocks, and are long enough to have totally dark areas and at least some troglophilic species (*Meta menardii* and *Calymmaria cavicola*, both spiders), but *C. vista* shows no cave modifications. Folding-door spiders (*Antrodiaetus* sp.) are very common in the immediate area.

Conotyla celeno n. sp.
Figures 43–45

Type. Holotype male collected December 12, 1965, by R. L. Hoffman, in vicinity of Comer's Rock, Iron Mt., ca. 4000 ft. (1300 m), Grayson-Wythe cos., Virginia. The specific epithet is a noun in apposition, and is the Greek name of one of the three Harpies of ancient mythology.

Diagnosis. Distinct from the other species of the *melinda* group in details of the gonopods, but is most easily separated from *vista* by the absence in *celeno* of an apophysis on the third joint of the first leg, and from *melinda* by the absence of apophyses on legs 6 and 7.

Description of holotype male. Length, 23.8 mm. Ocelli in triangular patch, in four rows plus single ocellus on right side, total of 19; in five rows on left side, total of 21. Antennal joints in order of length: 3, 4, 5, 2, 6, 7, 1. Leg 2 with distinct distal apophysis on the third joint; apophyses mesal in position on the femora of 3 and 4, apophyses of leg 4 the largest, distinctly capitate; apophysis of femur of leg 5 very small; legs 6 and 7 unmodified. Anterior gonopods (Figs. 43, 44) with lateral shoulder of normal size, lateral surface of lateral shoulder heavily pebbled; anterior and posterior branches subequal in size, anterior branch *in situ* curved around colpocoxite of posterior gonopod, anterior branch extending straight ventrad, heavily laciniated. Colpocoxites of posterior gonopods (Fig. 45) with terminal process thick, curved dorsal; lateral margin flared out as large, thin plate, lateral notch not at all developed; plumose area with a single branch; mesal tooth large, curved.

The *Atrolineata* Group

This group of two species may be generically distinct from *Conotyla*, but in my opinion are not sufficiently differentiated, although they have obviously had a long separate history—perhaps since the Pliocene droughts brought the Great Plains into being. They are characterized by reduced anterior gonopods, complex colpocoxites, and broadened posterior gonopod sterna.

Conotyla atrolineata (Bollman)
Figures 6, 46–50

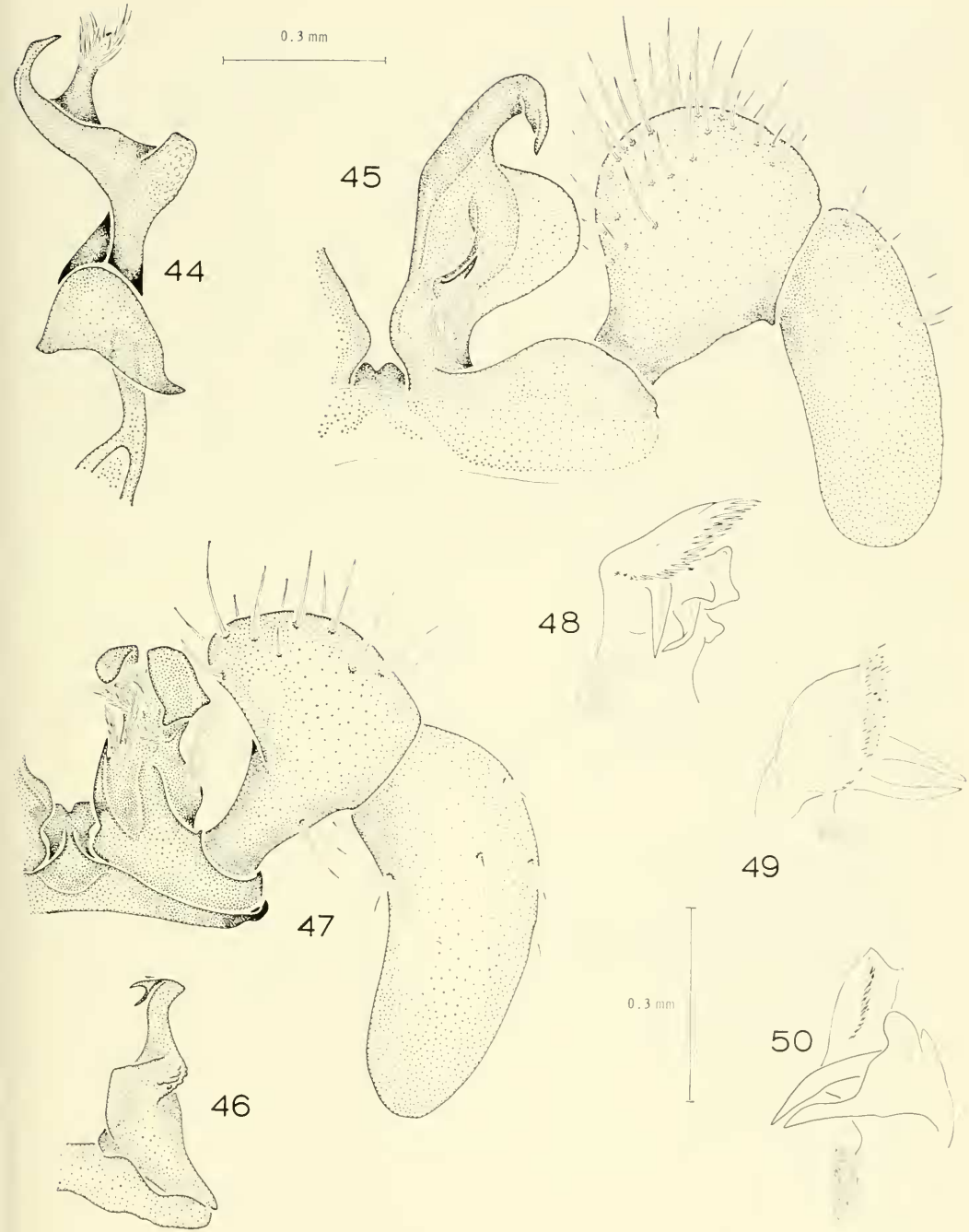
Craspedosoma atrolineatum Bollman, 1893, Bull. U. S. Nat. Mus., Vol. 46, pp. 35–36.

Conotyla atrolineata, Cook and Collins, 1895, Ann. New York Acad. Sci., Vol. 9, p. 75, figs. 95–100. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 98 (list).

Type. Male specimen from Glacier, British Columbia; assumed to be Glacier National Park, although the park was not established at the time the paper by Bollman was written (1887, 1893 dates the posthumous commemorative collection of Bollman's work). There is a Glacier post office in the park on the Canadian Pacific Railroad at the head of the Illecillewaet River. Type in U. S. National Museum, examined.

Diagnosis. Differing in the expanded sternum of the posterior gonopods from all species except *albertana;* from *albertana* in the much larger anterior gonopods and details of the colpocoxites of the posterior gonopods.

Description of male from Yoho National Park, B. C. Length, 15.5 mm. Eyepatches triangular, 20 ocelli in four rows on each side. Antennal segments in order of length: 3, 4 = 5, 2, 6, 7, 1. Leg 4 with large apophysis on femur, pregonopodal legs otherwise unmodified. Anterior gonopods



Figures 44–50. Male gonopods of *Conotyla* spp. Fig. 44–45. *Conotyla celeno*. Fig. 44. Left anterior gonopod, lateral view. Fig. 45. Left posterior gonopod, posterior view. Figs. 46–50. *C. atrolineata*. Fig. 46. Right anterior gonopod, anterior view. Fig. 47. Left posterior gonopod, posterior view. Figs. 48–50. Apical region of colpocoxite of posterior gonopod. Fig. 48. Posterior view. Fig. 49. Lateral view. Fig. 50. Mesal view.

(Fig. 46) with lateral shoulder lacking; large mesal lamella (posterior branch?) present; anterior branch curving around lateral surface of posterior gonopods *in situ*, tip three-pointed. Colpocoxites (Figs. 47–50) deeply cleft apically, posterior surface with two decurved lamellae and two prominent pointed branches; lateral pilose area present; mesal tooth sharp, pointed.

Notes. Known from several localities in the Rocky Mountains of eastern British Columbia; elevations between 4000 ft. and 5000 ft. in Yoho National Park, and from Robson Creek, Mt. Robson National Park (elevation unknown), in addition to the type locality. The continental divide separates this species from *C. albertana*, and it seems likely that they took refuge from the Cordilleran ice sheets on their present sides of the mountains, although there is no evidence of glacial refugia, other than possible isolated nunataks, in British Columbia.

Conotyla albertana Chamberlin
Figures 51–53

Conotyla albertana Chamberlin, 1920, Canadian Ent., Vol. 52, p. 167, fig. 17. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 98 (list).

Type. Male holotype from Bow River, Alberta, Canada; in Mus. Comp. Zool., examined. The Bow River flows from Bow Lake, just south of Bow Pass (6878 ft.) through Calgary, Alta., and joins the Oldman River to form the South Saskatchewan just north of Bow Island, Alta., a total course of more than 300 miles. Since most other known records for *C. albertana* are some 250 miles to the north of the river, it seems wise to here restrict the type locality to the banks of the Bow River in the vicinity of Lake Louise, Banff National Park, Alberta.

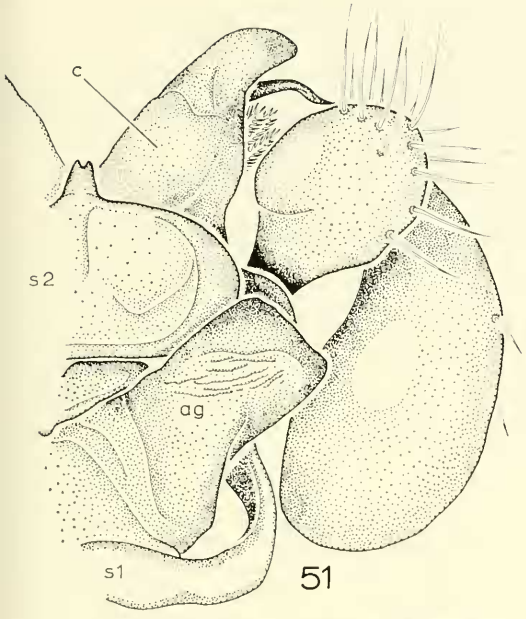
Diagnosis. Distinct from all but *atrolineata* in having the posterior gonopod sternum large, expanded and suboval, with prominent spiracles on the anterior surface, and in having the colpocoxites of the posterior gonopods with complex posterior surfaces. From *atrolineata*, *albertana* is distinct in the two-branched anterior gonopods, as described below.

Description of male from Jasper National Park, Alberta. Length, 11.0 mm. Eyepatches subhexagonal (truncate-triangular), five rows containing 18 ocelli on right side, 20 ocelli in five rows on left side. Antennal articles in order of length: 3, 4 = 5, 2, 6, 7, 1. Pregonopodal legs with slight apophyses on the femora of legs 3, 4, 5, 6; all mesal in position, heaviest on leg 4; apophysis of leg 6 very small. Anterior gonopods (Fig. 53) with lateral shoulder so well developed as to appear sigmoid; lateral shoulder rugose; anterior branch a heavy lamella, pressed against lateral side of sternum of posterior gonopod *in situ;* posterior branch curved, rodlike, sharply pointed. Posterior gonopods (Figs. 51, 52) with colpocoxites truncate, slightly curved posteriad, posterior surface with a complex group of smooth and plumose branches.

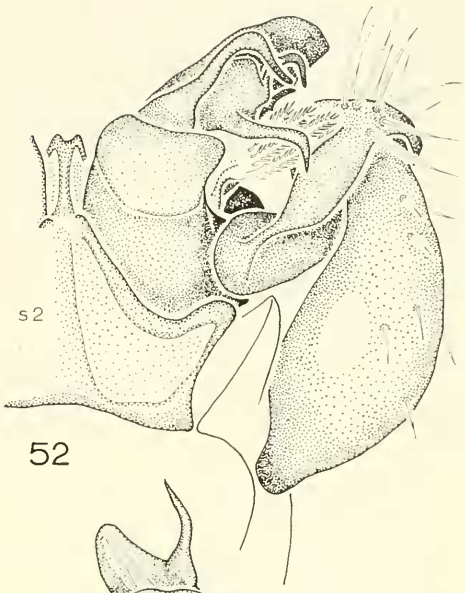
Notes. Aside from the type locality, this species is known from numerous specimens from several localities on Mt. Edith Cavell, including an alpine meadow, in Jasper National Park, Alberta, and Sulphur Mt. in Banff National Park. Unfortunately, the exact locality of some of the Jasper specimens was not indicated on the labels, only the altitudes (4500, 5000, and 5300 ft.). Since the tree line in western Alberta at the latitude of the park is from 7000–7500

→

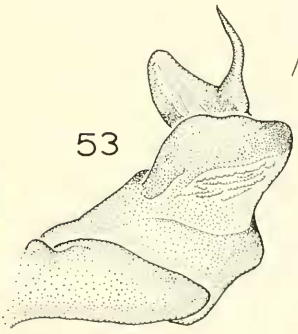
Figures 51–55. Male gonopods of *Conotyla* and *Achemenides*. Figs. 51–53. *Conotyla albertana*. Fig. 51. Right gonopods, anterior view. Fig. 52. Left gonopods, posterior view. Fig. 53. Right anterior gonopod, anteromesal view. Figs. 54–55. *Achemenides pectinatus*. Fig. 54. Right anterior gonopod and sternum, lateral view. Fig. 55. Basal region of anterior gonopods, anterior view.



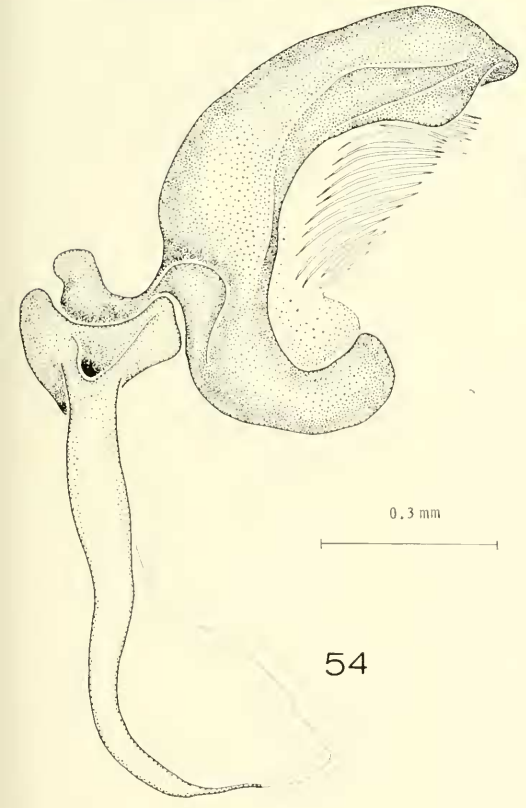
51



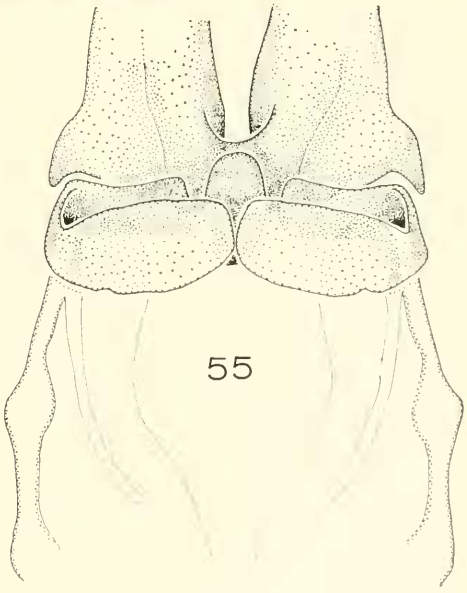
52



53



54



55

ft., depending on local conditions, it seems safe to assume that *albertana* inhabits the Canadian and Hudsonian Zones. During the Wisconsin glaciation, there may have been an ice-free refugial corridor between the Cordilleran and Keewatin ice sheets (Moss, 1955), into which *albertana* or its ancestral form may have retreated, but little is known of the vegetation of this corridor. From such a refugium, *albertana* may have re-invaded the montane regions.

Chamberlin's male holotype lacks the seventh legs; he failed to see the apophysis of leg 6. The posterior branch of the anterior gonopods is also missing in the holotype.

Genus *Achemenides* new genus

Type species. Conotyla pectinata Causey. The generic name (Greek, masculine) refers to a Greek marooned in a cave after the Trojan War.

Diagnosis. Medium-sized conotylids with somewhat reduced ocelli (14–17 in the single known species). Antennal segment 5 nearly twice as long as segment 4. Pregonopodal legs of male with apophyses on either third or fourth segments or both. Anterior gonopods fused at the base, drawn anteriad as a knob articulating with both lateral sternal plates. Sternum of the anterior gonopods divided, joined by a lightly sclerotized membrane; each sternal plate deeply cupped mesally, spiracle at lateral margin of cup, tracheal apodeme somewhat reduced. Posterior gonopods with the telopodite articles subequal; colpocoxites with two branches, the anterior laminate, the posterior rodlike. Sternum of posterior gonopods much reduced, bandlike, deeply curved posteriad between coxae; spiracle lateral, tracheal apodemes much reduced, bifurcate.

Distribution. Upper Mississippi River Valley, presently known only from caves and mines.

Species. One, the type species.

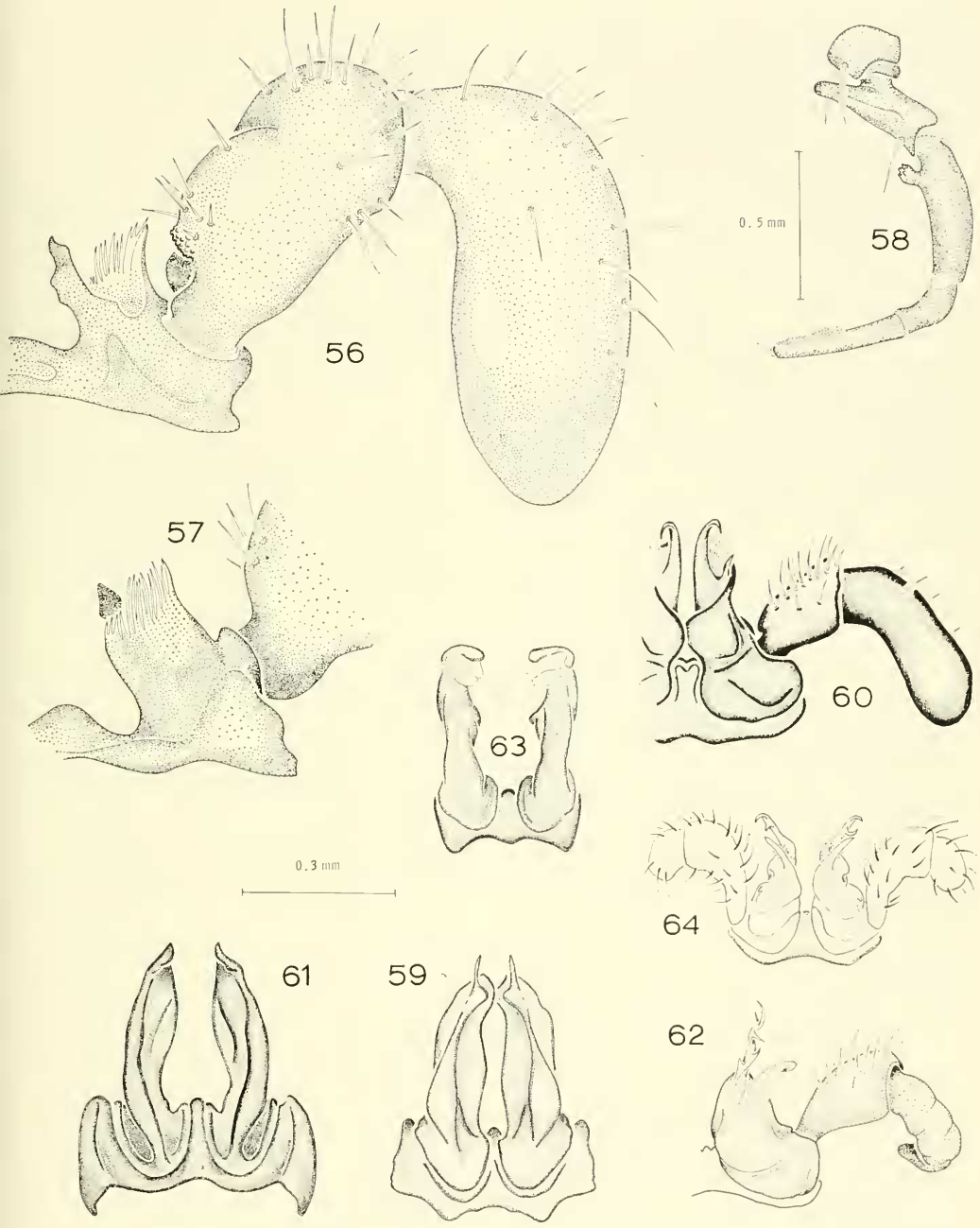
Achemenides pectinatus (Causey)
Figures 10, 54–58

Conotyla pectinata Causey, 1952, Proc. Biol. Soc. Wash., Vol. 65, pp. 112–113, figs. 4, 5. Chamberlin and Hoffman, 1958, U. S. National Mus. Bull. 212, p. 99 (list).

Sonoratyla pectinata Hoffman, 1961, Proc. Ent. Soc. Amer., Vol. 87, p. 268.

Type. Male holotype from "Smith Park, Mt. Carroll, Carroll Co., Illinois"; in collection of Illinois Natural History Survey, examined. Mr. Stewart Peck, who has had access to the field notes of H. H. Ross and M. W. Sanderson, collectors of the holotype male, informed me that the type locality was actually Smith Park Cave. As the type consists of only a dozen legless midbody segments, badly stained, and slide-mounted gonopods that could not be located, the description below is based on a specimen from the type locality identified by Causey and placed in the Illinois Natural History Survey Collection. The specific epithet is a Latin adjective referring to the comblike appearance of the anterior gonopods.

Description of male from Mt. Carroll, Illinois. Length, about 22 mm (specimen fragmented). Ocelli in three rows on each side, 14 in each triangular eyepatch. Antennal segments in order of length: 3, 5, 4, 2, 6, 7, 1. Legs 1 and 2 with slight swellings on the third joint, leg 4 with a weak apophysis (sometimes lacking) on the femur; legs 5 and 6 with strong distal apophyses on the femora; leg 7 with a capitate, toothed apophysis on the femur and a long, proximal lobe on the prefemur (Fig. 58). Anterior gonopods (Figs. 54, 55) very large, joined at base to form an anteriorly projecting curved knob; posterior surfaces with a thin, deeply laciniated ridge. Colpocoxites of posterior gonopods (Figs. 56, 57) with two divisions; an anterior deeply laciniated lamella and a posterior sagittiform branch; first telop-



Figures 56–64. Gonopods and associated structures of *Achemenides* and *Taiyutyla*. Figs. 56–58. *Achemenides pectinatus*. Fig. 56. Left posterior gonopod, posterior view. Fig. 57. Colpocoxite of right posterior gonopod, anterior view. Fig. 58. Right leg 7, posterior view. Figs. 59–60. *Taiyutyla corvallis*. Fig. 59. Anterior gonopods, posterior view. Fig. 60. Left posterior gonopods, posterior view. Figs. 61–62. *T. francisca*. Fig. 61. Anterior gonopods, posterior view. Fig. 62. Left posterior gonopod, posterior view. Figs. 63–64. *T. napa*. Fig. 63. Anterior gonopods, posterior view. Fig. 64. Posterior gonopods, posterior view.

odite joint with a low, rugose swelling on posterior mesal side.

Notes. I find the following discrepancies between the original description and the topotype specimen: the apophysis of leg 5 is on the fourth, not the third joint; leg 6 has a single lobe on the fourth joint, not two lobes on the third; leg 7 (Fig. 58) has apophyses on both the third and fourth joints, not just the third; there is no evidence of a "dorsal" (anterior) branch of the anterior gonopods; the deeply laciniate lamellae of the posterior gonopods are coxal, not sternal.

The reduced ocelli and fairly large size of this species indicate that it is somewhat adapted for a subterranean existence. *Austrotyla specus*, on the other hand, is troglophilic and shows no strong adaptations for cave life. Thus both could possibly occur in Smith Park Cave without competing directly. The locality needs to be recollected to confirm this, and to provide more specimens. The presence of this species at the edge of the classical Driftless Area, and in caves, is of great potential significance, especially since it shows a combination of conotyloid-austrotyloid features. But the problems associated with defining this area (Frye, 1965) limit speculation. Cushing (1965) found evidence of many disjunct arctic-alpine plants in the Driftless Area, and other plants that occur only south of the Wisconsin maximum farther east. It is not unlikely, therefore, that the region escaped glaciation, while the extreme climate drove *A. pectinatus* or its ancestor to seek refuge in the moderated climate of caves. In view of this unusual interest, I present a detailed list of new records below (see also Map 3).

Records. ILLINOIS: Jo Daviess Co., mines in North California Diggings, 7 mi. NW of Hanover, 31 October 1965, S. Peck, ♂♀♀; South Nicholsen Mine, 31 October 1965, S. Peck, ♂♂♀; Hutchings Mine, 5 mi. E of Galena, 30 October 1965, S. Peck, ♂♀. IOWA: Jackson Co., Hunter's Cave, 5 mi. N of Andrew, January–February 1966, S. Peck, ♂♂♀♀. WISCONSIN: Richland Co., John Gray Cave, 5.5 mi. NNE of Richland Center, no date, C. Krekeler, ♂.

Genus *Taiyutyla* Chamberlin, 1952

Taiyutyla Chamberlin, 1952, Nat. Hist. Misc., Chicago Acad. Sci. No. 113, p. 1. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 102. Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 270.

Type species. Taiyutyla corvallis Chamberlin, by original designation. The origin of the generic name, a neologism, is obscure. The gender is believed to be feminine.

Diagnosis. Small (8–11 mm in length) conotylids with the fifth antennal segment longer than the fourth, 20 ocelli or less in each eyepatch. Pregonopodal legs with apophyses on third or fourth article. Eleventh legs with prefemoral hooks. Anterior gonopods platelike, sometimes with terminal and subterminal processes or lamellae; sternum of anterior gonopods completely surrounding coxotelopodites, which articulate primarily on its posterior surface; spiracle prominent, in lateral depression. Posterior gonopods large, but slightly smaller to distinctly smaller than anterior gonopods, platelike or with two major branches, subterminal branch usually flattened, but sometimes spikelike, subtending or bearing a plumose-hirsute area; terminal branch or process short, or long and spirally curved, often bearing accessory teeth; no coxal depression, coxal bases swollen posteriorly. Sternum of posterior gonopods broad and deep anteriorly, thin and ribbonlike posteriorly; spiracles at proximolateral margins of broad, semicircular depressions. Telopodite articles of posterior gonopods variable, in some cases subequal and with second showing signs of segmentation, or with the first twice as long as the second, which is reduced to a small knob.

Species and distribution (Map 1). Three species in southern Oregon and northern California.

Key to Species

1a. Second telopodite joint of male posterior gonopods only half the length of the first (Fig. 64); leg 3 with an apophysis on the fourth joint, other pregonopodal legs unmodified ..... *napa*

1b. Second telopodite joint of male posterior gonopods (Figs. 60, 62) at least as long as the first; legs 4 through 7 and sometimes leg 3 with femoral apophyses 2

2a. Third leg of male with an apophysis on the femur; gonopods as in Figs. 61, 62; Marin Co., California ..... *francisca*

2b. Third leg of male unmodified; southern Oregon ..... *corvallis*

Taiyutyla corvallis Chamberlin
Figures 8, 59, 60

Taiyutyla corvallis Chamberlin, 1952, Nat. Hist. Misc., Chicago Acad. Sci. No. 113, pp. 1–2, figs. 1, 2. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 102 (list). Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 270, pl. 10, figs. 8, 9.

Type. Holotype from Corvallis, Linn Co., Oregon; in Chamberlin collection, Salt Lake City, Utah, could not be located.

Diagnosis. Unique in lacking an apophysis on the fourth joint of leg 3.

Description of male from Corvallis, Oregon. Length, 10.5 mm. Eyepatches triangular, three rows plus single ocellus, totaling 17, on right side; 20 ocelli in four rows on left side. Antennal articles in order of length: 3, 5, 4, 2, 6 = 7, 1. Legs 4 through 7 with apophyses on femora; apophyses on legs 4 and 5 very small, distal; apophysis of leg 6 strong, capitate, mesal; apophysis of leg 7 strong, capitate and toothed, promixal. Anterior gonopods (Fig. 59) larger than colpocoxites of posterior gonopods, subrectangular, flattened antero-posteriorly, slightly bent mesad, with aciculate subterminal process arising from a longitudinal ridge; lateral edges vaguely serrate. Sternum of anterior gonopods completely encircling coxotelopodites, produced between them as bilobed or trilobed condyle. Colpocoxites of posterior gonopods (Fig. 60) large and bulbous at base, ending in pointed terminal process, below which is a pilose area and a pointed subterminal process. Second joint of posterior gonopod with a distinct basal shoulder; third joint nearly twice as long as second.

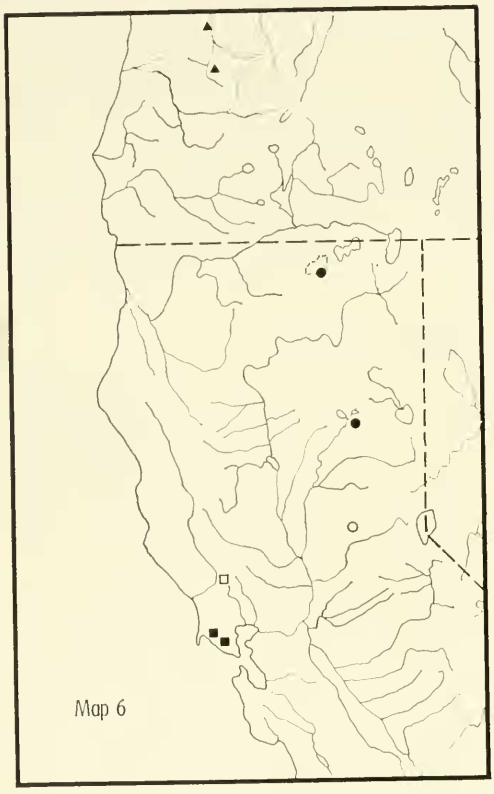
Notes. Nothing is known of the ecology and biology of this species, which is known only from the type locality (Map 6).

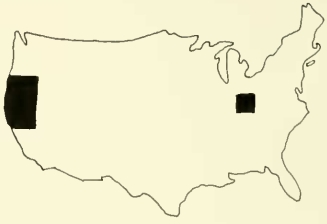
Taiyutyla napa n. sp.
Figures 63, 64

Type. Holotype male collected with two females and an immature specimen by Vincent Roth, 31 December 1953, Mt. St. Helena, Napa and Sonoma cos., California. The specific epithet refers to the type locality.

Diagnosis. In both *corvallis* and *francisca*, the second telopodite article of the posterior gonopods is longer than or as long as the first; in *napa* the second joint is less than half as long as the first. Only leg 3 has an apophysis on the fourth joint in *napa; corvallis* has leg 3 unmodified and *francisca* has apophyses on legs 4 through 7, as well as 3. The low swelling on the third joint of leg 2 present in *napa* is absent in the other two species.

Description of holotype male. Length, 8 mm. Eyepatches irregularly triangular, 3 irregular rows with a single ocellus totalling 18 on right side; 18 ocelli in four rows on left side. Antennal joints in order of length: 3, 5, 4, 2 = 6, 7, 1; joint 5 about twice as long as joint 4. Leg 3 with large distal apophysis on femur; leg 2 with a low, longitudinal swelling on the mesal side of third joint. Anterior gonopods (Fig. 63) curved posteriad distally, with prominent mesal shoulder about midway in their length, and with a thin, membranous subterminal lamina extending mesally. Colpocoxites of posterior gonopods (Fig. 64) intermediate between *corvallis* and *francisca*, subterminal process short, pointed; terminal process long, curved posteriad, with single accessory tooth. First telop-





Map 6. Northern California and southern Oregon, showing distribution of various conotylids; dots, *Plumatyla humerosa*, circle, *Conotyla extorris;* solid squares, *Taiyutyla francisca;* open squares, *T. napa;* triangles, *T. corvallis*, including *T. jonesi*.

Map 7. Southern Indiana, showing distribution of *Conotyla bollmani;* dots, epigean records; circles, cave records; dotted line, limit of Illinoisan glacial drift; broken line with dots, limit of Wisconsin glacial drift.

odite joint more than twice as long as second.

Notes. Nothing is known of the biology of this species, which is known only from the type locality (Map 6). Mt. St. Helena has a maximum elevation of 4344 feet.

Taiyutyla francisca n. sp.
Figures 61, 62

Type. Holotype male collected by C. W. O'Brien, 7 January 1962, one mile SE of Inverness, Marin Co., California. The specific epithet, a noun in apposition, refers to the proximity of the type locality to San Francisco Bay.

Diagnosis. Distinct from *corvallis* primarily in the form of the colpocoxites of the posterior gonopods, which bear spirally curved apical processes with several accessory teeth, also in the stronger modifications of legs 4 and 5 of the males.

Description of holotype male. Length 9.5 mm. Eyepatches triangular, 20 ocelli in four rows on left side, 20 ocelli in four rows and single ocellus on right side. Antennal segments in order of length: 3, 5, 4, 2, 6, 7, 1. Apophyses of legs 3 through 7 approximately same size, distal on leg 3 slowly becoming mesal on succeeding legs and proximal on leg 7. Anterior gonopods

(Fig. 61) large, flattened, terminal process blunt, slightly curved; large, thin mesal flange present. Colpocoxites of posterior gonopods (Fig. 62) smaller than anterior gonopods, complex; terminal process curved in a spiral of two turns, with four accessory processes as shown (Fig. 62); subterminal process a twisted, horizontal lamella finely laciniate on the posterior side. Second telopodite joint of posterior gonopod slightly longer than first, vaguely annulated.

Notes. Little is known of the biology of this species; the holotype was taken in a Berlese sample of *Pinus muricata* duff. See Map 6.

Genus *Austrotyla* Causey, 1961

Austrotyla Causey, 1961, Proc. Biol. Soc. Washington, Vol. 74, p. 260 (in part).
Sonoratyla Hoffman, 1961, Trans. Ent. Soc. Amer., Vol. 87, p. 269.

Type species. Of *Austrotyla*, *Conotyla specus* Loomis, by original designation; of *Sonoratyla*, *Conotyla montivaga* Loomis. The generic name is a feminine Latin-Greek neologism referring to the southerly distribution of the genus with respect to *Conotyla*.

Diagnosis. With the characters of the family. Anterior gonopod sternum appearing divided in some cases, but usually contiguous in the anterior and posterior midlines, or joined by sclerotic membrane. Anterior gonopods flattened, platelike, but with complex posterior surfaces; anterior gonopods covering colpocoxites of posterior gonopods *in situ*. Colpocoxites of posterior gonopods much smaller than anterior gonopods, usually with a single cupped lamella and a rodlike or platelike mesal branch, sometimes plumose. Pregonopodal legs with femoral lobes on legs 3 and 4 in all known species. Capitate lobes present on coxae of legs 10 and 11 in some species. Species usually pigmented, 20–24 ocelli in triangular patch.

Species. Five; distributed (Map 1) through Missouri and Illinois, Rocky Mountains from Alberta to Chihuahua (and possibly Queretaro). Separation of *specus* or its ancestors from the Rocky Mountain species may have occurred as early as the Pliocene, at the time of the formation of the Great Plains.

Key to Species

1a. Coxae 10 and 11 of males without lobes ..... *borealis*
1b. Coxae of legs 10 and 11 with lobes, or either coxa 10 or 11 lobed 2
2a. Lobe on coxa 11 only ..... *coloradensis*
2b. Lobe on coxa 10 3
3a. Lobe on coxa 10 only 4
3b. Lobes on both coxae 10 and 11 ..... *specus*
4a. Gonopods as in Figs. 68–70 ..... *montivaga*
4b. Gonopods as in Figs. 77–79 ..... *chihuahua*

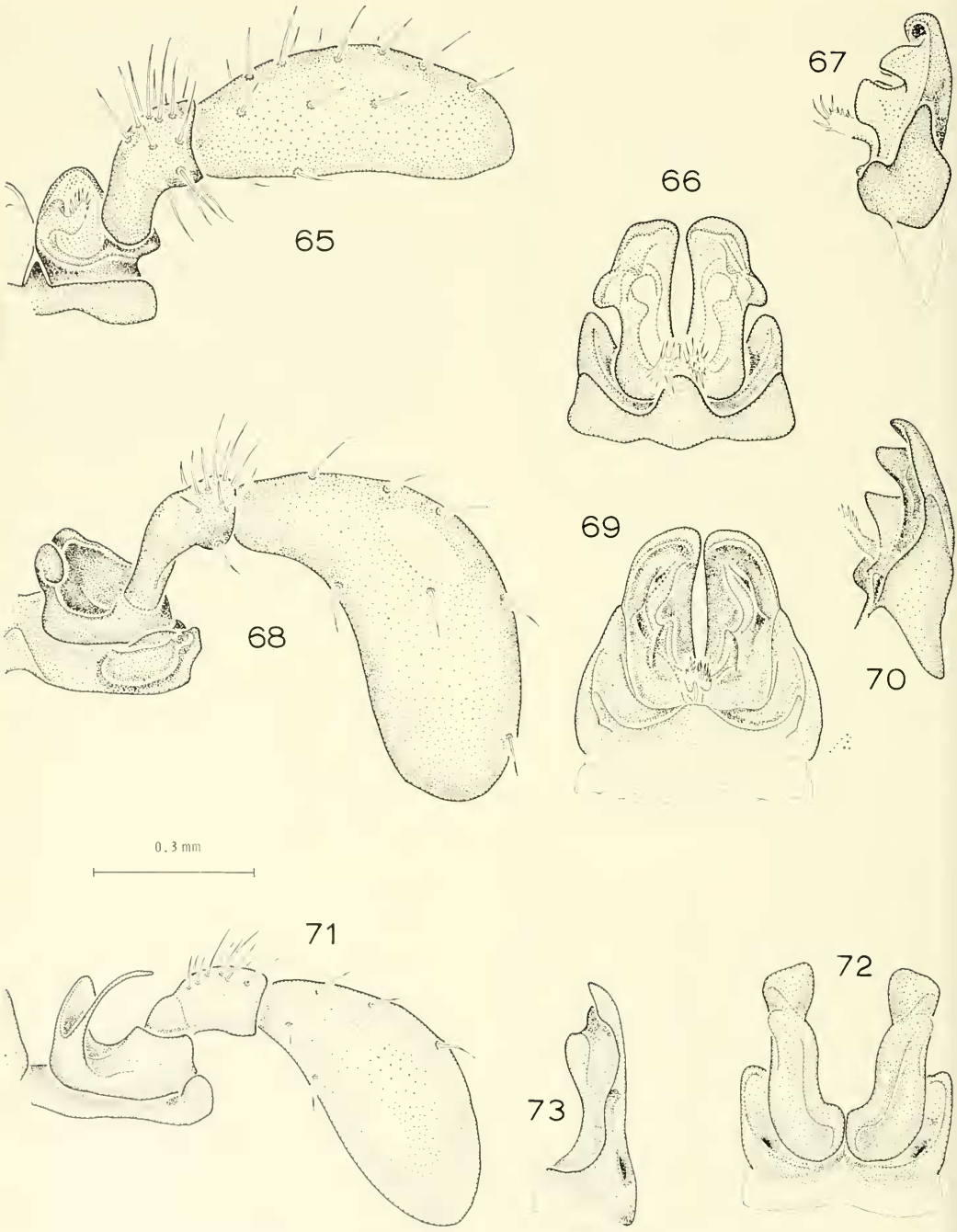
Austrotyla specus (Loomis) Figures 65–67

Conotyla specus Loomis, 1939, Bull. Mus. Comp. Zool., Vol. 86, p. 184, figs. 11a–c. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 99 (list).
Austrotylus specus specus, Causey, 1961, Proc. Biol. Soc. Wash., Vol. 74, pp. 260–264, figs. 5–10.
Austrotyla specus montivaga, (in part) Causey, 1961, Proc. Biol. Soc. Wash., Vol. 74, pp. 264–265.
Sonoratyla specus, Hoffman, 1961, Trans. Ent. Soc. Amer., Vol. 87, p. 269.

Type. Male holotype from Rice's Cave, 3 miles northeast of Goldman, Jefferson Co., Missouri, in Museum of Comparative Zoology, examined. The specific epithet is a noun in apposition (Latin: "cave") referring to the habitat of the type series.

Diagnosis. This species has much less complex anterior gonopods than *coloradensis* or *chihuahua*, and those of *borealis* are much simpler. In addition, the coxal processes of legs 10 and 11 are unique. See under *montivaga* for a discussion of differences between that species and *specus*.

Description of holotype male. Length, 11.5 mm. Eyepatches quadrangular, ocelli of both sides in three rows, 21 on the left side, 23 on the right, ocelli fully pigmented, not irregular in shape. Antennal articles in



Figures 65–73. Gonopods of *Austrotyla*. Figs. 65–67. *Austrotyla specus*. Fig. 65. Right posterior gonopod, anterior view. Fig. 66. Anterior gonopods, posterior view. Fig. 67. Left anterior gonopod, lateral view. Figs. 68–70. *A. montivaga*. Fig. 68. Right posterior gonopod, anterior view. Fig. 69. Anterior gonopods, posterior view. Fig. 70. Left anterior gonopod, lateral view. Figs. 71–73. *A. boreolis*. Fig. 71. Right posterior gonopod, anterior view. Fig. 72. Anterior gonopods, posterior view. Fig. 73. Left anterior gonopod, lateral view.

order of length: 3, 5, 4, 6, 2, 7, 1. Pregonopodal legs modified as described for the genus, legs 10 and 11 with anteriorly directed capitate lobes on the coxae. Anterior gonopods (Figs. 66, 67) with the sternal lobes evenly and heavily sclerotized, coxotelopodites with a lateral lobe above the sternal lobes; proximal laciniated branches large, prominent. Colpocoxites (Fig. 65) with the posterior lamella cupped and rounded distally, anterior branch sigmoid, laciniated distally; third telopodite joint twice the length of the second.

Notes. Both Causey and Loomis overlooked the lobes on the coxae of the 11th legs. Causey noted the variation in coloration and ocelli of this species, and a study of other populations indicates that both pigmented and unpigmented individuals occur in the same caves. Epigean specimens are rare; Causey reported them as *A. s. montivaga* from northern Illinois and Wisconsin. It seems likely that the same situation holds in this species as in *Conotyla blakei*, with troglophilic populations in the southern, lowland part of the range and epigean populations in the northern part. The absence of epigean records of either species in the regions of the cave populations may be due to a lack of collecting at the proper time, late fall, winter, and early spring, when these animals mature and are most active. Unpublished records kindly given to me by Stewart Peck include caves in Jackson Co., Iowa, and in the following Illinois counties: Jackson, Jo Daviess, Monroe, Saline, Henderson, and Union. Causey (1961) reported it from Franklin, Jefferson, and St. Clair cos., Missouri, and Sauk Co., Wisconsin (Map 3). An immature specimen in the Museum of Comparative Zoology from Blue Earth Co., Minnesota, strongly resembles *A. specus*.

Austrotyla montivaga (Loomis)
Figures 68–70

Conotyla montivaga Loomis, 1943, Bull. Mus. Comp. Zool., Vol. 92, pp. 383–384, figs. 4a–d. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 98 (list).

Sonoratyla montivaga, Hoffman, 1961, Trans. Ent. Soc. Amer., Vol. 87, p. 268, pl. 10, figs. 10–11.

Austrotyla specus montivaga, (in part) Causey, 1961, Proc. Biol. Soc. Washington, Vol. 74, p. 264.

Type. Male holotype from Santa Rita Mts., elevation 7500 ft., Pima Co., Arizona, in Museum of Comparative Zoology, examined.

Diagnosis. This species is much smaller than *coloradensis*, and the posterior surface of the anterior gonopods is much less complex; there is no clear area on the lateral sternal lobes as there is in *coloradensis* and *chihuahua*. Distinct from *specus*, which it closely resembles, in the details of the gonopods; in specimens I have examined, the third telopodite article is nearly three times as long as the second in *montivaga*, while in *specus* it is only slightly more than twice as long; there is no coxal lobe on leg 11 in *montivaga*, and one is present in *specus*.

Description of holotype male. Length, 9.0 mm. Causey (1961) described in detail the nonsexual characters of this species, but stated that the gonopods (Figs. 68, 69) were identical to those of *specus*. This is not the case. In posterior view (Fig. 69), the proximal laciniated lobes of *montivaga* are smaller, the ridges and lobes are less developed, and there is no lateral extension on the coxotelopodite above the insertion of the sternal lobes. The colpocoxites (Fig. 68) are less developed in *montivaga*, and the anterior branch is thicker and blunter. Otherwise, the description given by Causey (1961) is accurate.

Notes. Known from numerous specimens collected in the Santa Rita and Santa Catalina Mts., north and south of Tucson, Pima Co., Arizona. The type is from an elevation of 7500 ft., probably in or just below the *Pinus ponderosa* zone at the latitude of Tucson. The identity of specimens from Mescalero, New Mexico, could not be checked, as they were not available for study, but Chamberlin reported *colora-*

densis from Ruidosa, in the same mountains and only about 20 miles to the northeast. Which species (or an undescribed one) actually occurs in southern New Mexico awaits clarification. Both Loomis and Chamberlin might have assumed that their species was the only one in the Rocky Mountains; *coloradensis* males were not described until 1961. The records reported by Causey (1961) from Illinois and Wisconsin refer to epigean populations of *specus;* she stated that the gonopods were identical with *specus*, and placed *montivaga* as a subspecies of *specus*. A comparison of my figures of the holotypes of both species should establish their distinctness, besides the geographic difficulties of having a single subspecies with two populations separated by nearly a thousand miles of uninhabitable terrain.

Austrotyla borealis n. sp.
Figures 71–73

Type. Male holotype collected by D. Whitehead, 2–4 October, 1967, Jasper National Park, Alberta, "Sta. 5," 5300 ft. The specific epithet is an adjective indicating that it is the extreme northerly representative of its genus.

Diagnosis. This species is smaller than the other representatives of the genus, being about 9 mm long in mature males. The sterna of the anterior gonopods show very distinct angular shoulders while still attached to the telopodites, as in *specus*. The posterior surface of the coxotelopodites is simpler than in any other species, and there are no lobes on the coxae of legs 10 and 11.

Description of holotype male. Length, 9.8 mm. Eyepatches triangular; 24 ocelli on left side, in four rows plus single ocellus; four rows plus single ocellus totalling 22 ocelli on right side. Antennal segments in order of length: 3, 5, 4, 6, 2, 7, 1. Legs 3 and 4 modified as described for genus. Lateral lobes of the sterna of the anterior gonopods forming a distinct angular shoulder with the telopodites (Figs. 72, 73), with a distal area of very thin cuticle; spiracle on anterior surface, easily seen. Coxotelopodites of anterior gonopods simple, with single thickened ridge on posterior surface, ending in somewhat swollen knob. Colpocoxites of posterior gonopods (Fig. 71) with anterior branch long, filiform, branched. First telopodite joint is less than one third length of second telopodite joint. Coxae 10 and 11 without lobes.

Notes. Known only from the type locality. See notes on *Conotyla albertana* for further details on type locality.

Austrotyla coloradensis (Chamberlin)
Figures 74–76

Conotyla coloradensis Chamberlin, 1910, Ann. Ent. Soc. Amer., Vol. 3, p. 237, pl. 32, figs. 7–9, pl. 33, figs. 1–3. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 98 (list).

Austrotyla coloradensis, Causey, 1961, Proc. Biol. Soc. Washington, Vol. 74, pp. 254–260, figs. 2–4.

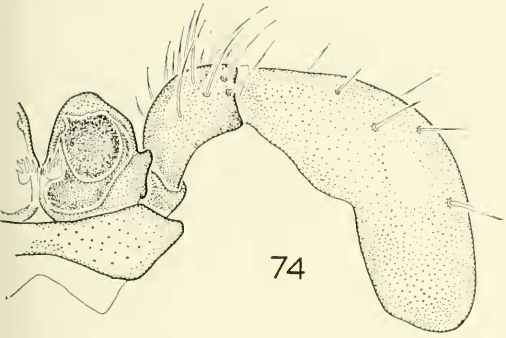
Type locality. Colorado. Causey (1961) designated a male neotype from Allen's Park, Boulder Co., Colorado, which is deposited in the Museum of Comparative Zoology, examined.

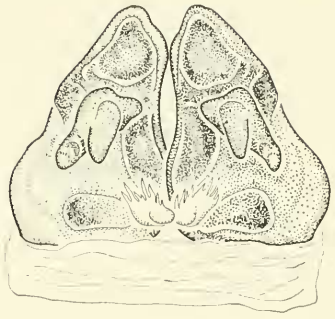
Diagnosis. Distinct in size and complexity of gonopods from all except *chihuahua*, but *coloradensis* has no anterior lobe on the coxa of leg 10. Distinct from *montivaga* by the larger size and much more prominent lateral shoulders.

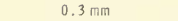
Description of neotype male. Length, 15.7 mm. Eyepatches triangular, 23 ocelli on each side in four rows plus single ocellus. Antennal articles in order of length: 3, 5, 4, 6, 2, 7, 1. Pregonopodal legs modi-

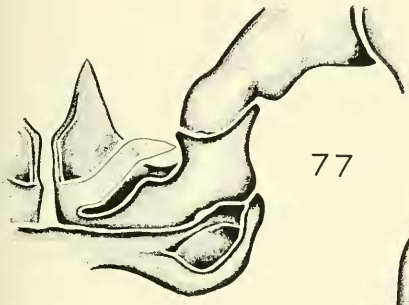
→

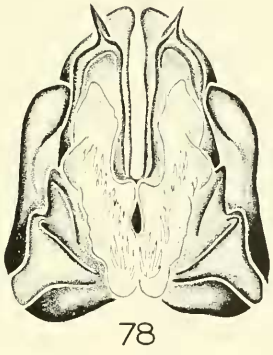
Figures 74–81. Gonopods of *Austrotyla* and *Plumatyla*. Figs. 74–76. *Austrotyla coloradensis*. Fig. 74. Right posterior gonopod, anterior view. Fig. 75. Anterior gonopods, posterior view. Fig. 76. Left anterior gonopod, lateral view. Figs. 77–79.

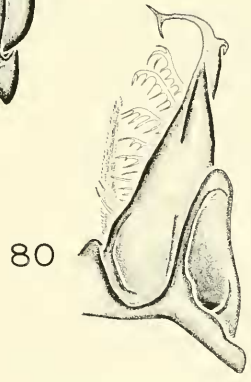


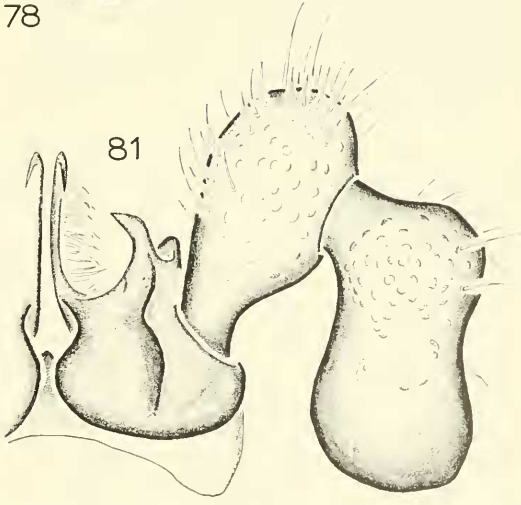












A. chihuohua. Fig. 77. Colpocoxite of right posterior gonopod, anterior view. Fig. 78. Anterior gonopods, posterior view. Fig. 79. Left anterior gonopad, lateral view. Figs. 80–81. *Plumatyla humerosa*. Fig. 80. Right anterior gonopod, anterior view. Fig. 81. Left posterior gonopad, posterior view.

fied as described for genus, apophysis of leg 3 somewhat larger than that of leg 4. Anterior gonopods (Figs. 75, 76) thin, lamellate, bearing posteriorly a prominent knob near the midline of each telopodite and a mesal laciniated branch; sternal lobes with a semicircular area of very thin cuticle that appears to be a hole at low magnification. Colpocoxites of the posterior gonopods (Fig. 74) relatively large, deeply cupped, posterior lamella deeply notched laterally, anterior branch small, lightly laciniated; second telopodite joint twice the length of first.

Notes. Causey's (1961a) drawings of the gonopods, made from cleared, slide-mounted material, leave something to be desired. The thin area on the sternal lobes is represented as an open space, and the tracheal apodeme is shown as being coalesced with the sternal lobe high up on the coxotelopodite. In actuality, the tracheal spiracle, not seen by Causey, is easily visible on uncleared preparations and is at the lateroanterior corner of the sternum, whence it leads normally into the tracheal apodeme. The horizontal portions of the sternites meet in the anterior midline as well as the posterior, rather than being represented entirely by a membranous area. The colpocoxites of the posterior gonopods in Causey's illustration show neither the deep lateral cleft in the posterior lamella, nor the short, mesal plumose branch. See Causey (1961a) for emendations in Chamberlin's original description, based on a female.

There is some variability in size in this species, but it could not be connected with any geographical trend. The smallest specimens were about 16 mm long and the longest were close to 23 mm long.

Known from numerous specimens from the following Colorado counties (Map 4): Larimer, Jackson, Eagle, Pitkin, Chaffee, Gunnison, Hinsdale, Mineral, and Conejos. Probably also occurs in southern Wyoming and northern New Mexico. The majority of records are from coniferous forests above 7000 ft. elevation.

Austrotyla chihuahua n. sp.
Figures 77–79

Type. Male holotype from 100 m above Rio Urique, 84 km south of Creel, Chihuahua, Mexico, collected February 28, 1966, by J. Reddell and W. Bell. The specific epithet is a noun in apposition, referring to the type locality.

Diagnosis. The posterior surface of the anterior gonopods is complex, as in *coloradensis*, but the colpocoxites of the posterior gonopods of *chihuahua* have the posterior lamella angular and the anterior branch large, flattened and reflexed; *chihuahua* has a coxal lobe on leg 10, while *coloradensis* has none.

Description of holotype male. Length, 14.0 mm. Eyepatches truncate-triangular, 23 ocelli in four rows on left side, 21 ocelli in four rows on right side. Antennal articles in order of length: 3, 5, 4, 2 = 6, 7, 1. Legs 3 and 4 modified as described for genus, apophyses slightly larger than in other species. Sterna of anterior gonopods as in *coloradensis;* gonopods (Figs. 78, 79) almost contiguous in midline, distinctly depressed mesally on anterior surface; posterior surface with complex knobs and plumose branches. Colpocoxites of posterior gonopods (Fig. 77) with posterior lamella triangular; anterior branch flattened, reflexed. Coxa of leg 10 with an anterior lobe.

Notes. Nothing is known of the biology of this species, which is known only from the type locality.

Genus *Plumatyla*, new genus

Austrotyla Causey, (in part) 1961, Proc. Biol. Soc. Washington, Vol. 74, p. 260.

Sonoratyla Hoffman (in part) 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 269.

Type species. Conotyla humerosa Loomis; the generic name is a Latinized

Spanish-Greek neologism derived from the related genus *Conotyla* and Plumas Co., California, type locality of the type species. The gender is feminine.

Diagnosis. With the characters of the family. Anterior gonopod sternum intermediate between *Taiyutyla* and *Austrotyla*, heavily sclerotic throughout, with lateral lobes extending laterad to coxotelopodites, but incomplete posteriorly, as in *Conotyla*. Anterior gonopods with two major branches, the anterior largest and set mesally with small laciniate processes; posterior branch a simple hirsute rod. Posterior gonopod sternum broadened and depressed laterally. Colpocoxites of posterior gonopods with a large mesal branch bearing laciniations as in anterior gonopod; anteroposterior lamella heavily sclerotized. Femoral lobes on some pregonopodal legs. Species troglobitic, without pigment, ocelli about 10, in two rows.

Species. One, found in mines and caves in northern California.

Plumatyla humerosa (Loomis)
Figures 80, 81

Conotyla humerosa Loomis, 1943, Bull. Mus. Comp. Zool., Vol. 92, pp. 384–385, figs. 5a–d.

Type. Male holotype and other specimens collected Sunnyside Mine, 3 mi. SW of Seneca, Plumas Co., California, January 22, 1923, by H. S. Barber; deposited in U. S. National Museum, examined; immature male paratype in Museum of Comparative Zoology.

Diagnosis. See generic diagnosis.

Description of topotype male. Length, 16.0 mm. Ocelli in two rows, 9 ocelli on left side, 8 ocelli on right side. Antennal segments in order of length: 3, 5, 4, 2, 6, 7, 1. Legs 5, 6, and 7 with prominent femoral lobes. Anterior gonopods (Fig. 80) larger than colpocoxites; posterior branch bears a subterminal lateral hook and is distally bifid; posterior branch rodlike, densely pilose. Posterior basal knob fits into sternal cavity of posterior gonopods. Colpocoxites of posterior gonopods (Fig. 81) with two branches, anterior mesal branch hooked posteriad, small laciniated branches on lateral surface; posterior lateral branch a subtriangular, curved, well-sclerotized lamella. Tracheal apodemes of both gonopods reduced in size.

Notes. The only other mature specimens known to me, excepting the specimens from the type locality kindly lent to me by N. B. Causey, are from Indian Wells Ice Cave, Lava Beds National Monument, Siskiyou Co., California. They differ from the holotype and paratype by being smaller (13–14 mm), lacking a lobe on the femur of leg 5, and having the anterior branch of the anterior gonopod slightly more attenuate. Otherwise, the gonopod structure is identical to the Sunnyside Mine specimens. For this reason, I hesitate to describe it as a distinct species. Immature representatives of *Plumatyla* are known from a number of mines, limestone caves, and lava tubes in northern California and adjacent Oregon. Only the collection of mature specimens can indicate the range of variation and the number of species in this genus. The lava tubes in Lava Beds National Monument may be as old as 60,000 years (Gale, 1959). The local glaciation of the northern California area during the late Pleistocene (Detling, 1968) may have been responsible for the cave habitat of these animals.

LITERATURE CITED

Barr, T. C. 1968. Cave ecology and the evolution of troglobites. Evol. Biol., **2**: 35–102.

Brölemann, H. W. 1935. Myriapodes Diplopodes (Chilognathes I) *Faune de France*, 29, Paris. 368 pp.

Buckett, J. S., and M. R. Gardner. 1967. A new family of cavernicolous millipedes with the description of a new genus and species from Idaho (Diplopoda: Chordeumida: Chordeumidea). Michigan Ent., 1(4): 117–126.

Causey, N. G. 1952. Four new chordeumid millipeds from the United States (Nematophora, Chordeumidea). Proc. Biol. Soc. Washington, **65**: 111–118.

———. 1961a. *Austrotyla*, a new milliped genus (Chordeumidea: Conotylidae: Conotylinae). Proc. Biol. Soc. Washington, **74**: 251–266.

———. 1961b. *Adrityla*, a new milliped genus (Chordeumidea: Conotylidae). Psyche, **68**: 131–136.

Chamberlin, R. V. 1941. New western millipeds. Bull. Univ. Utah, Biol. Ser., **6**(5): 3–23.

———. 1951. Eleven new western millipeds. Natur. Hist. Misc. No. **87**: 1–12.

———. 1952. Two Oregon millipeds of the Order Chordeumida. Nat. Hist. Misc., No. **113**: 1–3.

Chamberlin, R. V., and R. L. Hoffman. 1958. Checklist of the millipeds of North America. U. S. Nat. Mus. Bull., **212**: 1–236.

Cook, O. F. 1896. On recent diplopod names. Brandtia, **2**: 8.

Cook, O. F., and G. N. Collins. 1895. The Craspedosomatidae of North America. Ann. New York Acad. Sci., **9**(1): 1–100.

Cushing, E. J. 1965. Problems in the Quaternary phytogeography of the Great Lakes region. *In* H. E. Wright, Jr. and D. G. Frey [Ed.] The Quaternary of the United States. Princeton, N. J.: Princeton University Press, pp. 403–417.

Detling, L. E. 1968. Historical background of the flora of the Pacific Northwest. Bull. Mus. Nat. Hist. Univ. Oregon, **13**: 1–57.

Frye, J. C., H. B. Willman, and R. F. Black. 1965. Outline of the glacial geology of Illinois and Wisconsin. *In* H. E. Wright, Jr. and D. G. Frey [Ed.] The Quaternary of the United States. Princeton, N. J.: Princeton University Press, pp. 43–61.

Gale, R. R. 1959. Geology of Lava Beds National Monument. Bull. Nat. Speleol. Soc., **21**(2): 62.

Hoffman, R. L. 1961. Systematic and morphological notes on North American conotyloid Diplopoda. Trans. Amer. Ent. Soc., **87**: 259–272.

Hoffman, R. L. 1963. Notes on the structure and classification of the diplopod family Heterochordeumatidae. Ann. Mag. Nat. Hist., **13**(6): 129–135.

Howden, H. F. 1963. Speculations on some beetles, barriers, and climates during the Pleistocene and Pre-Pleistocene periods in some non-glaciated portions of North America. Syst. Zool., **12**(4): 178–201.

Loomis, H. F. 1939. The millipeds collected in Appalachian caves by Mr. Kenneth Dearolf. Bull. Mus. Comp. Zool., **86**(4): 165–193.

———. 1943. New cave and epigean millipeds. Bull. Mus. Comp. Zool., **92**(7): 373–410.

Moss, E. H. 1955. Vegetation of Alberta. Bot. Rev., **21**: 493–567.

Schubart, O. 1934. Tausendfüssler oder Myriapoda. 1: Diplopoda. *In* Die Tierwelt Deutschlands, 28 Teil. Jena: Gustav Fischer, 318 pp

Shear, W. A. 1969. Cave milliped genera of the United States. Psyche, **76**(2): 126–143.

Verhoeff, K. 1913. Ascospermophoren aus Japan Zool. Anz., **43**: 342–370.

———. 1932. Diplopoden-Beitrage (124. Diplopoden-aufsatz). Zool. Jahrb., Syst. Arb., **62**: 469–524.

———. 1942. Ascospermophoren aus Japan und über neue japanische Diplopoden. Zool. Anz. **137**: 201–217.

Wayne, W. J., and J. H. Zumberge. 1965. Pleistocene geology of Indiana and Michigan. *In* H. E. Wright, Jr. and D. G. Frey [Ed.] The Quaternary of the United States. Princeton N. J. Princeton Univ. Press, pp. 63–83.

(*Received 10 October 1969.*)

INDEX

Valid generic and species names in italics; only major discussions listed for species.